Lettura "G. Quagliariello"

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Some Recent Developments in the Neurobiology of Consciousness

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Consciousness is an ill-defined philosophical and psychological concept which has been traditionally eschewed by biology and by the neurosciences in particular. The difficulty to identify objective behavioral criteria for consciousness, the diffidence against introspection as a reliable means of scientific knowledge, and the separation between conscious and unconscious processes as a threat to the concept of the unity of the living organism are all factors that have acted as deterrents to a biological approach to consciousness. But recently the description and interpretation of new findings in the fields of perception and memory have made it necessary to resort to a large-scale use of the term consciousness, with a resulting considerable increase of its occurrence in neuroscience articles and textbooks. For example, in the popular neuroscience textbook edited by Kandel and colleagues, the term consciousness does not appear in the analytical index of the first edition (1981), while it or equivalent terms appear six times in the second edition (1985), seven times in the third edition (1991), and as many as thirty-two times in the fourth edition (2000). In an article entitled "Consciousness and Neuroscience", Crick and Koch (1998) have forcefully argued that 'the problem of the neural correlate of consciousness is now ripe for direct experimental attack'. What has brought about such a major change in the attitude of neuroscientists toward consciousness? A primary cause for this shift can be identified in the discovery that visually guided behavior can occur in the absence of any awareness of the visual cues that provide guidance to the behavior, and that while several memory traces are fully conscious, others that are not can nevertheless reveal their existence through overt behavior. The extension of these kinds of investigations to normal subjects in appropriate experimental settings has allowed to obtain evidence for similar dissociations between what one does and what one knows. The modern means of non-invasive visualization of cerebral processes during cognitive tasks have further extended the understanding of the neurobiology of consciousness by demonstrating the involvement of distributed cortical and subcortical systems in the fusion of the memory of the past, the cognition of the present and the expectations for the future in a unitary experience. Language is a fundamental element of consciousness, but its absence does not exclude the possibility that animals with a complex nervous system (especially primates and marine mammals), preverbal children and aphasic patients exhibit behavioral activities fully classifiable as conscious. A bona fide self-consciousness is probably limited to the human species and its emergence occurs around an age of twenty months, but some rudiments of self recognition in a mirror can be demonstrated in chimpanzees.

The distinction between conscious and unconscious memories, and its importance for the re-emergence of consciousness in the neurosciences, has been the object of an extensive authoritative review (Milner et al., 1998). The present review will be restricted to analyses of visual capacities that have forced the investigators to use the term consciousness in order to distinguish different classes of visual behaviors. In drawing heavily from a chapter by the author that has recently appeared in another publication (Berlucchi, 2004), the review will also be restricted to evidence provided by behavioral data especially from brain damaged subjects. Readers interested in the contributions to explorations of conscious processes and mechanisms from modern techniques such as brain imaging and non-invasive brain stimulation are referred to other recent research papers and reviews (e.g. Zeki and fftyche, 1998; Zeman, 2001, 2004; Culham and Kanwisher, 2001; Rees et al., 2002; James et al., 2003; Juan et al., 2004).

Visual consciousness and unconscious visually guided behavior

Patients with primary visual cortex lesions are able to emit appropriate motor or verbal reactions to visual inputs from the supposedly blind contralesional part of their visual field, in spite of their proclaimed unawareness of those inputs. They can, for example, move their eyes or point to, or even name, visual targets that they deny seeing (reviews in Stoerig and Cowey, 1997; Weiskrantz, 1998). The term blindsight, which was originally coined to denote those reactions, is now used to refer to all forms of visually guided behavior that are not accompanied by related conscious visual experiences. Blindsight behavior can be observed in patients with various neurological disorders, other than damage to the primary visual cortex, and even in normal subjects submitted to specific kinds of visual stimulation (e.g. Milner, 1995; Milner and Goodale, 1995; Kolb and Braun, 1995; Driver and Mattingley, 1998; Marcel, 1998; Savazzi and Marzi, 2002; Goodale et al., 2004). Many blindsight phenomena have been described in

patients with unilateral brain damage and a clinical contralesional hemianopia, extinction or neglect, all conditions that involve an absence of conscious awareness of stimuli in the visual field contralateral to the lesion. Evidence for blindsight is provided not only by overt behavioral responses to otherwise unperceived stimuli in the contralesional visual field, but also by the effects of such unperceived stimuli on the processing of consciously perceived stimuli from the ipsilesional visual field. "Unseen" light stimuli presented in the abnormal visual field can modulate the characteristics of responses to concurrent light stimuli from the good field (Marzi et al., 1986; Corbetta et al., 1990). As an example, the detection of a simple flash stimulus in the intact visual field ipsilateral to a complete hemispherectomy can be significantly speeded up by the simultaneous presentation of an identical flash stimulus in the opposite hemianopic field, even when the latter stimulus is by itself incapable of eliciting any overt response, whether concious or unconscious (Tomaiuolo et al., 1997). Likewise, patients with severe contralesional neglect have been shown to improve their discrimination of patterned stimuli in the intact visual field as a result of the previous presentation in the neglected field of stimuli identical to or belonging in the same category as the target. The occurrence of the facilitating stimuli was consistently denied by the patients, and no facilitation was obtained with stimuli physically and categorically unrelated to the targets (Berti and Rizzolatti, 1992). Yet another approach was employed by Danckert et al. (1998) with a patient with a hemianopia contralateral to a one-sided occipital lesion who consistently denied seeing letter and color stimuli presented in his hemianopic field. Nevertheless, the patient's reaction time for verbal identification of a consciously perceived letter or color stimulus was prolonged if an incongruent flanker letter or color stimulus was simultaneously presented in the hemianopic field, suggesting that the seemingly unperceived color and letter information from the latter field was unconsciously processed up to a degree that could interfere with the processing of consciously seen targets. Finally, discrimination of the emotional expression of a half face in the intact visual field was found to be facilitated by the simultaneous presentation to the blind field of a half face with a congruent expression, whereas discrimination of the expression of whole faces in the intact field was interfered with by incongruent facial expressions presented in the blind field (de Gelder et al., 2001).

Conversely, there is evidence to suggest that blindsight can be enhanced by the influence of visual information processed by intact brain systems, to the extent that unconscious detection of light stimuli in an impaired hemifield can be facilitated by concurrent stimuli in the intact hemifield (Ward and Jackson, 2002), possibly through attentional processes started by the consciously perceived stimuli in the latter hemifield (Kentridge et al., 1999). Stimuli in the intact field may even confer conscious awareness to stimuli in the impaired field, as suggested by the finding that in hemianopic patients no after-images are experienced if visual stimulation is limited to the blind field, whereas bilateral complementary stimuli give rise to veridical bilateral afterimages (Torjussen, 1978) or even bilateral perceptions (Marcel, 1998).

Blindsight phenomena in visual agnosia

Blindsight has also been reported in patients with severe visual agnosia from diffuse cortical damage who display a severely impaired conscious vision and a preserved unconscious guidance of action towards visual targets. These findings have provided a basis for general hypotheses about an at least partial separation between the neural substrates for perception and those for action (Milner, 1995; Milner and Goodale, 1995; James et al., 2003; Gooale et al., 2004). The hallmark of cortical visual agnosia is usually a profound inability to identify and discriminate visual objects, whereas perception of color and visual motion, as well as general visual imagery, can often be preserved to at least some degree (Milner and Goodale, 1995; Servos and Goodale, 1995; Zeki et al., 1999). Aglioti et al. (1999) have investigated whether preserved color vision can not only provide cues that help the patient to arrive at conscious inferences about the identity of visual objects, but also bring out by itself blindsight responses to visual shapes. A patient suffering from a bilateral parieto-occipital cerebral atrophy and a dense apperceptive agnosia was consistently unable to identify and discriminate even simple visual shapes and objects, such as single large black letters presented against a white background. In contrast, his color perception was nearly normal. He consistently reported a distinct awareness of the color stimuli that he was asked to point to or name, and his visual imagery was intact. In an attempt to assess whether the patient's fully conscious chromatic vision could bear out some latent, implicit or explicit capacity for the processing of visual shape, Aglioti et al. (1999) used a simplified version of the Stroop test using single letters. In the standard version of the Stroop test, normally seeing subjects are comparatively fast in naming the color in which a word is written if the word matches the name of the color, and comparatively slow if the word denotes a competing color. The effect is best accounted for by an incongruency between the response activated by the color stimulus and the response activated by the word stimulus, the well learned and presumably automatic tendency to read the word being liable to interfere with the production of the competing color-naming response (MacLeod, 1991). Regan (1977) had shown that a robust Stroop effect could be obtained in normal subjects with the presentation of appropriately colored single letter stimuli corresponding to the initials of color names. Aglioti et al. (1999) confirmed this finding and applied the test to above described agnosic patient. The test involved repeated discriminations between two colors, red and green, and two letters, a capital R and a capital V, i.e. the initials of the Italian words "rosso" for "red" and "verde" for "green". In a forced-response paradigm, there were a letter discrimination task, which required speeded choice responses involving the pressing of a key to the letter R and another key to the letter V, regardless of their color; and a color discrimination task, which required

speeded key-pressing responses to the red color and the green color, regardless of whether the colors were carried by an R or a V. In the color task there were no statistical differences in either accuracy or RT between congruent and incongruent stimuli. In contrast, in the letter task accuracy was at chance with the incongruent stimuli, as it had been in many previous tests of letter recognition, but it was clearly and significantly above chance with the congruent stimuli. Further, overall RT of correct responses was significantly longer for incongruent stimuli than for congruent stimuli. Thus, the agnosic patient did not exhibit a standard Stroop effect insofar as, according to the expectation, his performance on the color discrimination was unaffected by the letter stimuli, which he consistently seemed unable to perceive. However, the accuracy of his responses to letter stimuli showed a clear effect of the congruency or incongruency of the color stimuli with the letters to be discriminated. His capacity for letter discrimination remained at chance with color-incongruent letter stimuli, whereas a successful discrimination clearly emerged with color-congruent letter stimuli. That such performance reflected a real potential for letter discrimination was supported by the faster response speed to color-congruent than to color-incongruent letter stimuli. Throughout the testing the patient consistently reported that he had no conscious awareness of the letter presented on any given trial, so that his better-than-chance ability to discriminate such stimuli and his greater speed of response to color-congruent than color-incongruent letters could legitimately qualify as blindsight.

This finding can tentatively be accounted for by the hypothesis that the patient's preserved visual imagery would allow perceived colors to activate an orthographic representation of the corresponding word name, which would in turn activate the orthographic representation of the word's component letters. Viewed as a top-down influence, this activation would act on any existing ability for visual processing of letters by giving an advantage to inputs consistent with the activated letter representation over inputs inconsistent with it. It thus seems possible that in the case of an input consistent with the activated letter representation, the advantage afforded to that input could bear out a partial residual ability of the patient for the implicit processing of letters. Inconsistency between the input and the activated letter representation, and the resulting absence of a top-down support would preclude the emergence of a successful letter discrimination even with the protracted processing attested by the patient's very long response times.

In more general terms, the processing of visual information transmitted by a damaged system may be enhanced by intact visual processes to a degree that results in blindsight, as in the case of Aglioti et al. (1999), or even in conscious experiences. Potential top-down controls that can strengthen the signal in a damaged visual system are the so called feedback cortico-cortical connections from higher-order visual cortical areas to lower-order ones, or even cortical projections to subcortical visual centers such as the superior colliculus. According to Lamme (2001), unconscious visually guided behaviors can be executed on the basis of entirely feedforward input-output transformations, whereas conscious vision would also require the action of feedback inputs from higher order cortical areas to the primary visual cortex.

The role of the primary visual cortex in conscious visual perception

This is a debated topic. The main problem is not whether visual consciousness arises in the primary visual cortex (Crich and Koch, 1995), but whether it is possible to be aware of a visual stimulus that does not activate the primary visual cortex. Stoerig and Barth (2001) have suggested that some kind of low-level phenomenal vision is possible even without the primary visual cortex. Similarly, a recent study by Weiskrantz et al. (2002) indicates that there may be forms of conscious vision that do not require the primary visual cortex. In a patient with unilateral damage of that cortex, contralesional visual stimuli such as gratings, colors, shapes, etc. that could elicit blindsight responses (i.e. correct discriminations associated with denial of stimulus awareness) could also give rise to consciously experienced negative after-images after being turned-off. These delayed subjective experiences might be accounted for by the time necessary for feedback cortico-cortical connections to act on residual substrates for conscious vision in the damaged hemisphere.

The problem may be similar to that of the role of the primary somatosensory cortex in the awareness of one's own body, an important element of that self-consciousness which seems to be a prerogative of the human species. Some rudiments of self consciousness are perhaps present in chimpanzees, who share with humans the ability of mirror self-recognition (de Veer et al., 2003). In the 19th century the psychologist William James stated in his book "Principles of Psychology" that the nucleus of the self is always the bodily existence felt to be present at the time, and that the entire feeling of one's own mental activities is really a feeling of bodily activities, mainly in the head (motor adjustments of eyeballs, eyelids and eyebrows) and the throat (changes of breathing due to movements of the soft palate, posterior nares, glottis, and so on). All these abilities suggest the existence of a mental construct, termed corporeal or body awareness, which comprises the sense-impressions, perceptions, memories and ideas about the dynamic organisation of one's own body and its relations to that of other bodies. According to Melzack (1990), corporeal awareness relies upon a large neural networks where somatosensory cortex, posterior parietal lobe and insular cortex play crucial and different roles, as indicated by the effects of selective lesions in this network. However, while lesions of the primary somatosensory cortex induce deficits in the tactile and proprioceptive domains, there is no evidence that they can cause alterations of higher-order body awareness. These are instead produced by lesions of the posterior parietal cortex or the insula, indicating a closer associations of these brain regions with conscious representation of the body compared to the primary somatosensory cortex (Berlucchi and Aglioti, 1997).

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