Figure 1 (Fischer). The Zöllner illusion: the long lines do not appear as parallel. Fixate the point in the middle and observe the lines becoming parallel.

reflexive saccades (errors) occur in an antisaccade task (Weber et al. 1998). About half of these saccades and their retinal consequences escape the subjects' consciousness: they are neither reported verbally nor indicated by key press (Mokler & Fischer 1999).

1. The simple geometrical arrangement of lines in Figure 1 show the famous Zöllner illusion: the long lines do not appear as parallel though they are so in reality. The reader may now try to fixate the point in the middle and attend to the lines in the periphery. After some seconds of stationary fixation one clearly sees the lines becoming parallel. No question, both ways of looking – with and without saccades – represent conscious vision. Yet, they lead to different results. Interestingly, it is the saccade mode which leads to the illusion, while the fixation mode results in the correct perception. Scanning through the known geometrical illusions, quite a number of them were found to disappear with stationary fixation (Fischer et al. 2001b). In fact, one may argue that these illusions are not illusions at all, because the visual system as such provides the correct percept. (By the way, it is not clear why these disillusions have escaped the awareness of scientists for more than a hundred years.)

In any case, the exact kind of sensorimotor activity in the actual visual process – saccades or fixation – determines the conscious perceptual result. One could also argue that only inactivity – no oculomotor activity (= fixation) – leads to the correct result. It would be very interesting to see how this observation of geometrical illusions fading with fixation can be incorporated in the theory of sensorimotor contingency. Clearly, a simple neural representation cannot explain the observation unless one introduces an extra mechanism for the geometrical distortion resulting from saccades.

2. The instruction to make saccades from an initial fixation point in the direction opposite of a suddenly presented stimulus is called the antisaccade task (Hallett 1978). One can manipulate the condition so as to make it rather difficult for the subject to follow the instruction: if the initial fixation point is extinguished before a stimulus is presented to the right or left (gap condition), the strength of fixation is diminished and the reflexes become relatively stronger. In this situation subjects generate prosaccades to the stimulus in about 10–15% of the trials (Fischer & Weber 1992). These saccades are unwanted and happen against the subjects' conscious decision.

If the subjects were given a visual precue which indicated the direction and position to which they have to make the next saccade (an antisaccade), the rate of errors increased unexpectedly by a factor of 2 or 3 (Fischer & Weber 1996); even though, ac-

cording to the classical view, attention should have been captured by the cue and should have facilitated the wanted antisaccade, the opposite happened. In addition, if the subjects were asked to indicate by a key press at the end of each trial whether they believed that they made an error on that trial, 50% of the error saccades escaped the subjects' conscious perception: they denied that they made the error saccade and the corresponding corrective saccade of double size. When the eye movement traces were analysed separately for trials with recognized and unrecognized errors, it turns out that reaction times of the error saccades were the same but the correction times were shorter for unrecognized than for recognized errors (Mokler & Fischer 1999).

Moreover, subjects did not realize that they had been looking at the stimulus for 50 to 200 msec with their fovea. Here we have a twofold misperception: the saccades remained unconscious and the position of the stimulus was misperceived. In those trials the subjects reported a perception of what they wanted to do, not what they really did. They also perceived consciously what would have happened to the stimulus if they had made the correct intended eye movement.

In a few other trials the subjects reported an error but did not make one (false alarm). In these trials the subjects may have shifted their attention to the stimulus and experienced these shifts as saccades. In agreement with the notion that a covered shift of visual attention is a time consuming process the reaction time of these misperceived correct antisaccades were considerably longer than those of correctly perceived correct antisaccades (Mokler & Fischer 1999).

It should be noted that both visual phenomena considered here are independent of any theoretical concept such as, for example, the assumption of neural representations. They are just observations which one way or another should have a place in a valid theory of conscious vision.

## Mirror neurons: A sensorimotor representation system

Vittorio Gallese and Christian Keysers
*Istituto di Fisiologia Umana, Università di Parma, I-43100 Parma, Italy.*
**vittorio.gallese@unipr.it     keysers@nemo.unipr.it**

**Abstract:** Positing the importance of sensorimotor contingencies for perception is by no means denying the presence and importance of representations. Using the evidence of mirror neurons we will show the intrinsic relationship between action control and representation within the logic of forward models.

The paper by **O'Regan & Noë** (**O&N**) addresses the issue of visual perception from a stimulating perspective, by emphasizing the crucial role played by action in perception. Historically, perception and action have been studied all too separately. A recent instantiation of the intrinsic relationship between action and perception is provided by the discovery of mirror neurons: mirror neurons, although found in motor areas, are endowed with visual properties matching the execution of an action with its perception (Gallese 2001; Gallese et al. 1996; Rizzolatti et al. 1996; Umiltà et al. 2001).

Although the perspective offered by **O&N** is stimulating, we are afraid that the conclusions they draw on mental representations are overstretched. One of their central claims is that there is no need for an inner representation of the outside world. To make their point the authors refer, amongst others, to the work by Lenay (1997) on photoelectric sensing in blind people. In Lenay's experiment, "at a given moment during exploration of the environment, subjects may be receiving no beep or vibration whatever, and yet 'feel' the presence of an object before them. In other words, the experience of perception derives from the potential to obtain

changes in sensation." The subjects, having no supernatural way of sensing the presence of the object, must therefore derive their feeling of its presence from some form of knowledge about the object's location. This knowledge, in turn, must derive from past experience. O&N would probably argue that this knowledge reflects mastery of the laws of sensorimotor contingency. But in our eyes, what this implies is that the perception of an object must derive from a representation of it in the brain, albeit not an iconic one.

Indeed, representations in the brain are not thought by visual neuroscientists to be point-by-point picture-like representations. Representations of objects in the temporal cortex, for instance, have been shown to correlate with perception (Keysers et al. 2001), and yet they clearly represent the world in a very abstract, feature-based way, where entire faces are represented by the firing of single neurons, and not by the firing of a set of neurones arranged in the shape of a face. Hence, in our eyes the merit of focusing on the relevance of sensorimotor contingencies for perception – in contrast to what **O&N** suggest – is not to falsify the importance of representations for perception but to help us understand the nature of these representations. In particular, it points towards the fact that representations may take the form of forward models of motor consequences (see Kawato 1999; Wolpert 1997; Wolpert et al. 1995). Mirror neurons may be examples of forward models as representations (Gallese 2001): they respond, for instance, to the sight of a hand action and to the intention to execute it. Hence, they may constitute a system that can predict the sight of the agent's hand action when planning to move its hand – and thereby their activation also constitutes a "visual" representation of a hand action. This representation can be used not only to control your own actions, but also to perceive those performed by others. Visual representations and motor representations may thus be two sides of the same coin (Gallese 2000). By this account, representations are not an end but a means: the payoff of the necessity to anticipate, and therefore re-present, the consequences of a planned action in order to control it better. How else could we know that our intended action is going wrong if we didn't have an inner representation of what it should look like? Ironically, in a way mirror neurons instantiate both the very expertise of sensorimotor contingencies so central to O&N's theory, and the representation of the world, the importance of which O&N argue against.

These representations are not the result of a solipsistic monadic organism, but rather the result of the active and dynamic interplay of the organism with its environment and the control requirements of this interplay.

In conclusion, we think that stressing the importance of sensory motor contingencies in perception is not antagonistic to the notion of an inner representation of the world, but rather a way to help us understand how such representation may be achieved and why it exists.

## Real action in a virtual world

Melvyn A. Goodale

*Department of Psychology, University of Western Ontario, London, Ontario N6A 5C2, Canada.* **mgoodale@uwo.ca**
**http://www.sscl.uwo.ca/psychology/faculty/goodale/**

**Abstract:** O'Regan & Noë run into some difficulty in trying to reconcile their "seeing as acting" proposal with the perception and action account of the functions of the two streams of visual projections in the primate cerebral cortex. I suggest that part of the problem is their reluctance to acknowledge that the mechanisms in the ventral stream may play a more critical role in visual awareness and qualia than mechanisms in the dorsal stream.

Who couldn't be enthusiastic about **O'Regan & Noë**'s (**O&N**'s) proposal? They have managed to push the idea of "seeing as act-

ing" much further than many of us might have thought possible. All those thorny problems – representation, consciousness, qualia – vanish from sight as soon as one realizes that vision is more about doing than seeing and that our percepts are more virtual than real.

The central concept of **O&N**'s proposal is that seeing is a specific way of exploring the environment. There is no need to posit a detailed internal representation of the outside world; vision arises because of the perceiver's knowledge of the sensorimotor contingencies that are jointly determined by the visual apparatus and the visual attributes of objects. The idea that perception is a grand illusion and that the external world represents itself is an attractive one – but there are still some issues with respect to experiential perception and the visual control of action that are only partially addressed in O&N's otherwise compelling thesis.

**O&N**'s treatment of the ventral-dorsal story is particularly unconvincing. They begin by arguing that the double dissociation in deficits following lesions of the dorsal and ventral streams poses no problem for their "seeing as acting" idea. But then they go on to say something rather curious. "Seeing" they say "is an activity depending on a range of capacities, for example, capacities for bodily movement and guidance, on the one hand, and capacities for speech and rational thought on the other." Thus, they argue, it is not surprising that these capacities "can come apart" and that the dorsal stream "can operate in relative isolation from the ventral stream."

But what does this mean? Are they harking back to the point that they raised earlier in the article, that visual awareness depends on both mastery of sensorimotor contingencies and the use of this mastery in one's planning, reasoning, and speech? Do they want to associate the sensorimotor part of this equation with the dorsal stream and the reasoning part with the ventral stream? But if so, then it would be difficult to reconcile this idea with the pattern of deficits seen in patients with ventral or dorsal stream damage. If visual awareness depends on both sensorimotor contingencies and the ability to use the mastery of these contingencies for rational thought then patients should lose visual awareness with lesions of either the dorsal or the ventral stream. But we know that this is simply not the case. Patients with ventral-stream damage are much more likely to lose visual awareness of particular visual attributes than are patients with dorsal-stream damage. Patients with dorsal-stream damage, who may have lost a good deal of visuomotor control, are still quite aware of the shape, size, orientation, and location of objects that they see (for review, see Goodale & Milner 1992; Milner & Goodale 1995). In other words, there is something about visual processing in the ventral stream that is more intimately associated with seeing than is processing in the dorsal stream.

But alternatively, perhaps **O&N** mean to say that the activity of seeing – visual awareness – supports both the guidance of action and the guidance of thought. Thus, according to O&N, the visual-agnosia patient DF, who suffered ventral-stream damage, has partial visual awareness of form. As they put it, DF "is unable to describe what she sees, but she is otherwise able to use it for the purpose of guiding action." But this distinction does not capture the profound nature of DF's problem. It is not that she cannot talk about what she sees; she cannot perform the simplest of visual discriminations of form. She cannot, for example, distinguish horizontal from vertical lines or tell if two simple geometrical shapes are the same or different. But at the same time, she has excellent visual imagery for form and is also able to draw familiar objects and shapes from memory (much like a blind person might do). Moreover, she can readily identify an object using haptic exploration. What she appears to lack is any conscious appreciation of the visual form of objects. Yet when she reaches out to grasp objects that vary in size, shape, and orientation, her grasp is oriented correctly and the posture of her moving hand reflects the geometry of the object well before she makes contact with it. In short, she shows nearly perfect visuomotor control in the absence of any evidence that she actually "sees" the form of the object she is grasping.