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The rose and the fly. A conjecture on the origin of consciousness

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ABSTRACT

The Scottish philosopher Thomas Reid and more recently the evolutionary psychologist Nicholas Humphrey argued for a basic distinction between sensation (*what is happening to me*) and perception (*what is happening out there*) with the former, but not the latter, being associated with consciousness. Conscious experiences in this view would emerge from changes in the state of the body, i.e. as bodily actions, and would maintain such a primal characteristic nowadays. I argue that the evolutionary reason for the sensation/perception distinction can be traced back to organisms' movement, and to the consequent need to tell apart two varieties of an otherwise identical local stimulation: namely, either as the outcome of external stimuli passively impinging on body surface or as the outcome of an organism movement giving rise to encountering with external stimuli. The Erich von Holst *Reafferenzprinzip* effectively modelled such a distinction by postulating that an efference copy is generated in association with the motor command thus nullifying any sensory signal that arises as a by-product of an organism movement. I argue that if sensation originally equates to a bodily action (or its internalized representation), then it could be that an efference copy of local (or internalized) bodily action is generated under stimulation and compared to that associated with active motor command. This way the result would be leaving sensation (what is happening to me) or nullifying it and leaving only perception (what is happening out there) depending on whether or not a motor command has occurred. Implications of this hypothesis for the presence of consciousness in animals or other organisms such as plants are briefly discussed.

1. On the use of anyone else's toothbrush

The minimal requirement for the appearance of consciousness seems to be a proper topic in a Special issue devoted to minimal cognition. Here I consider consciousness as phenomenal experience, namely that it may feel something to have mental states such as pain, seeing red, or smelling a rose. Of course, not all cognition needs to be conscious. I argued elsewhere that the issue of how and why we are having experiences or feelings cannot be equated with cognition, i.e. with possession of higher cognitive abilities [1,2]. There is plenty of evidence that advanced forms of cognition can be observed in the absence of consciousness (e.g., [3,4]). Besides we usually do not deny the possession of conscious experiences to human beings that, because of severe acquired or inherited disabilities, would appear incapable of even elementary forms of cognition (e.g., [5]).

Here I would like to discuss briefly one particular aspect of the problem, namely the reason why conscious experiences may have made their appearance in the natural world. If my argument is correct, then it could provide some hints as to the kind of creatures that may plausibly possess consciousness.

Nicholas Humphrey, who will be one of the main characters of this paper, in his book "*Soul Dust*" ([6] p. 7) wrote that theorists tend to treat other people's ideas about consciousness like toothbrushes—no self-respecting person wants to use anyone else's. Quite in contrast I'll be trying here to make good use, and possibly some progress, from other people's theories, and more specifically from two of them: the one that posits a basic distinction between sensation and perception, and the one that introduces the mechanism of an efference copy (*Efferenzkopie*) to account for some features of our sensory world.

2. The rose of Thomas Reid (and Nicholas Humphrey)

The first idea I am going to discuss should be ascribed to the

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Scottish philosopher Thomas Reid (1710–1796), and it has been marvelously developed in the hands of evolutionary psychologist and neuropsychologist Nicholas Humphrey [6–8]. Reid conceived cognition of external objects as comprising two different aspects, the awareness of the object being perceived, and the belief in the existence of the object perceived.

«The external senses have a double province; to make us feel, and to make us perceive. They furnish us with a variety of sensations, some pleasant, others painful, and others indifferent; at the same time they give us a conception, and an invincible belief of the existence of external objects. This conception of external objects is the work of nature. The belief of their existence, which our senses give, is [also] the work of nature; so likewise is the sensation that accompanies it. This conception and belief which nature produces by means of the senses, we call perception. The feeling which goes along with the perception, we call sensation … When I smell a rose, there is in this operation both sensation and perception. The agreeable odour I feel, considered by itself, without relation to any external object is merely a sensation … Perception (in contrast) has always an external object; and the object of my perception, in this case, is that quality in the rose which I discern by the sense of smell.» ([9], 1:318).

And again:

"… the smell of a rose signifies two things: First, a sensation, which can have no existence but when it is perceived, and can only be in a sentient being or mind; Secondly, it signifies some power, quality, or virtue, in the rose, or in effluvia proceeding from it, which hath permanent existence, independent of the mind, and which, by the constitution of nature, produces the sensation in us. By the original constitution of our nature, we are both led to believe that there is a permanent cause of the sensation, and prompted to seek after it; and experience determines us to place it in the rose." ([9], I, 114).

In simpler words, when I smell a rose I have both a sensation and a perception: the sensation is the conscious (and pleasurable, in this case) experience of the smell that I feel, as something occurring to my body, without any relation with the existence of an external object, just a bodily change, whereas the perception is the recognition of the presence of an object, the rose itself, out there.

Schopenhauer (1788–1860) maintained a somewhat similar distinction, stating that sensation would represent a change in the state of the body, something occurring « on or under the skin » which involves no reference to anything outside the body in which it occurs. In contrast, perception represents external objects, namely things outside one's body (see [10]). Note also that according to Schopenhauer we are first aware of our sensations and only then, after a rational act that makes use of causal relationships, we inferred the existence of an external object [10].

Nicholas Humphrey [7] was the first to argue persuasively that such a distinction between sensation and perception, which got unnoticed in most circumstances in ordinary life, proves to be apparent in certain neurological conditions. Specifically, in the condition of blindsight, in which people can properly behave toward a visual stimulus (e.g. pointing to its spatial location) whereas at the same time denying to sense anything [3,11]. Humphrey argued that the reverse condition, that of unaffected sensation with perception instead being impaired is shown in agnosia [6–8].

According to Reid and Humphrey a basic feature of sensation is its nature of bodily response, of modification in the state of the body. «*Sentition*» is the term invented by Humphrey to indicate an affective response to stimulation occurring at the body surface [7,8]. According to Humphrey, being sentient should have been the same, at the origin, with being locally reactive, i.e. "*responding selectively at the place where the surface stimulus occurred*" ([7], p. 142). Then during evolution, this "*doing something about the stimulus at the point of stimulation*" would have come to involve signals travelling to and from more centrally placed parts of a nervous system, and finally in human beings and possibly in other organisms "*the response has come to involve signals going all the way from the body surface to the brain and back again*" ([7], p. 143) being at that point completely internalized.

One wonders, however, what is the origin, in evolutionary terms, of such a distinction between sensation and perception. The issue is quite relevant assuming Reid/Humphrey are correct with their claim that only sensation is conscious. For it would seem plausible to imagine that organisms can react to stimuli in a proper way – i.e. with a bodily response - without this being accompanied by any conscious feeling. Why then in evolutionary history the distinction between a sensation (conscious) and a perception (not necessarily conscious) would have taken place?

3. The fly of Erich von Holst (*via* Steinbuch, Helmholtz, von Uexküll and several others…)

In 1950 Erich von Holst, with his student Horst Mittelstaedt, carried out a simple though quite extraordinary experiment. They twisted the neck of a blowfly (*Eristalis* a genus of hoverflies of the family Syrphidae) turning its head through 180° along its longitudinal axis, thus making the positions of the two eyes reversed. The fly behaved quite strangely under these circumstances, circling either clockwise or counterclockwise at random [12]. In a similar vein, Roger Sperry [13] rotated surgically 180° the eye of a fish (*Sphoeroides spengleri*) and observed too that the animal circled around to the left or to the right until it stopped and freezed in an atypical posture. Both researchers come out with a similar idea – termed *Efferenzkopie* or *efference copy* by von Holst and Mittlestaedt, and *corollary discharge* by Sperry – according to which every time the brain generates a command to move, a duplicate copy of the signal is sent also to the sensory system. The brain would thus use the efference copy to make a comparison between the expected movement and the actual movement, a feedback mechanism to ensure correct movement in the intended direction. When the signals from the sensory system arrive to the comparator in the brain from a twisted head or a twisted eye the feedback mechanism would magnify the error instead of correcting it, thus causing the animal to keep circling unable to correct itself from feedback.

The biological significance of the mechanism is familiar to scholars of human visual perception: the motion signal falling on the retina could be due to either something moving in the visual field or to the motion of the eyeball. How can the visual system tell them apart? The answer is that when the organism is engaged with active movement, for instance it has initiated an eye movement, the brain cancels out the expected movement on the retina keeping subjectively the image steady. When, in contrast, something is moving in the environment, and there is no efference copy of a motor command, motion is seen.

The idea that perceptual mechanisms mainly evolved to make the control of action as straightforward as possible is well recognized (e.g., [14,15]). It is thus likely that our phenomenal experience of the world may be closely related to the mechanisms we use to act upon it. Note that the idea of an efference copy provides a general solution to a ubiquitous problem for organisms that move actively, that of disentangling the otherwise identical sensory inputs generated by something happening to them (sensation) from those generated by something happening out there (perception). Consider the earthworm's dilemma as it has been put forwards by Merker ([16], p. 90).

«Earthworms display a swift withdrawal reflex to cutaneous touch (…). It is mediated by giant fibers in the segmented worm's ventral nerve cord. Consider the worm's initiation of a crawling movement. Such a movement will produce sudden stimulation of

numerous cutaneous receptors ("re-afference," …), yet no withdrawal reflex is released to abort the movement. Apparently the worm's simple nervous system discounts cutaneous stimulation contingent on self-produced movement as a stimulus for withdrawal.»

Merker [16] stressed that the mechanism for making this functional distinction may be purely peripheral, and that the earthworm "*has solved a simple version of a problem that will only grow in magnitude with evolutionary advances in the sophistication of movement and the complexity of sensory systems that guide it*" (p. 90). He thus concluded that consciousness arose in organisms with a centralized brain. However, what seems interesting to me here is the possibility that the efference copy provides the biological rationale and the mechanism for the distinction between sensation and perception, originally posited by Reid.

The development of locomotion has entailed a new kind of problem for animals: the need to discriminate two varieties of the stimulation, which are not distinguishable in terms of the effect they exert on membranes, but which are distinguishable in terms of their origin. In order to determine this origin a circuit is necessary that re-sends the command for the motor action to the sensory system that must decide on what is being received. At this point, I believe, the stimulation on the membrane becomes an explicit feeling, because now the organism must distinguish between what happens to it and what happens out there, that is, the organism must actively represent itself with respect to the outside.

There is no need to make such a distinction, and therefore to have sensations, as long as there is no possibility of misunderstanding. The story as Reid and Humphrey told us holds up even for a fissile organism: the organism would respond (without feeling anything) with local contraction of the body and, since it is not actively moving, it does not need to represent any object out there, for it has no way to act on external objects. The very moment the organism does develop this capacity, with active movements, and a conception of «something out there » goes along with what happens on the surface of the body, then it has *to feel* what difference it makes when something happens to itself and when something happens out there [17].

The origins of the general idea of a *Reafferenzprinzip* dates back well before von Holst and Sperry (see [18] for a complete historical account). It was anticipated, among others, by Bell, Purkinje, Helmholtz, von Uexküll, and the physiologist Johann Georg Steinbuch (1770–1818), who hypothesized an interaction between the motor mechanisms for the active control of hands (which he dubbed as *Bewegidee,* i.e. the idea of the movement) and the afferent sensory signals from receptors associated with active tactile stimulation of an object in order to account for the lack of tactile recognition (or attenuated touch, see e.g. [19]) when passive stimulation of mechanoreceptors occurs (instead of active movements by e.g. the fingers of a hand).

The link with the distinction between sensation and perception can be easily conveyed with some simple experimental phenomenology. Let's consider two situations of apparently similar sensory stimulation on a finger. One in which you move your finger to touch an object, and one in which the same object passively stimulates your finger. In the former situation you feel an object out there (perception), in the latter you feel something *on* your finger (sensation). In the first case only with an active effort of attention you can shift from perceiving the external object to feeling the stimulation *on* your skin. The difference is likely to be associated with the action of an efference copy of the motor command which is generated in the first case, nullifying any sensation on the finger, but not occurring at all in the second case.

My argument is simply that before the evolution of the feedback circuit of the efference copy, the touch of an object on the surface of the body produced only a local bodily reaction. It is only after the invention of the efference copy, made necessary by the development of active locomotion, that the bodily reaction counts as a sensation, i.e. that it begins to feel.

The hypothesis that the efference copy may offer a basic rationale and scope for the distinction between self and not-self, and therefore for the appearance of consciousness has been argued for by several authors. Godfrey-Smith [20] for example, stressed that efference copies is a way for organisms to use their own actions to feed perception (p. 154). However, it seems to me that only if the idea of the efference copy is linked with the distinction between sensation and perception it can be useful in explaining the origins of sensation, and therefore of consciousness. The next section will elaborate on this aspect.

4. How to make von Holst's fly landing over Reid's rose

Let's go back to the example of the tactile stimulation on the finger. The idea of the efference copy can effectively explain the cancelling of the local sensation during an active movement because the stimulation can be accounted for in terms of the motor command to move the finger. However, how come a sensation (something occurring to me) is there when a passive stimulation occurs to the finger? According to Reid and Humphrey a bodily response (or its internalized neural version) occurs at the surface but the issue is that this was true also before the development of the efference copy. So why should the organisms exhibit conscious sensation rather than simply performing a bodily response at the surface without feeling anything? Why should the organism feel anything when there is no efference copy/corollary discharge, namely when the sensory signal comes out undisturbed from the comparator? It seems as if the efference copy could contribute to the appearance of perception but it remains unclear why it should be related to sensation. We need to find a way to get Erich von Holst's fly to rest on Thomas Reid's rose.

One hypothesis could be that time plays a crucial role. The efference copy anticipates the arrival of the sensory signal, so when the sensory signal comes in and there is no efference copy waiting for it, only a time lapse for the operation of the comparator will be needed. This time lapse, the time needed to compare the signals in the comparator, could perhaps account for the fact that the sensation has always a minimum duration [21].

Taylor [22] argued that the corollary discharge signal is held in a temporal memory and that this short staying, before its annihilation following the arrival of the sensory signal to the comparator, could provide the sensory signal with a sense of ownership and agency that defines conscious experience. In order to obtain this, Taylor introduces a complication, namely the idea that the corollary discharge is no longer simply derived from the motor signal, but from attention. This corollary discharge of the «movement of attention » would be retained in a working memory by supplying the properties of the experience to the sensory signal before being canceled by it (see also [23,24]). The difficulty, in my view, is that in this way the properties of the experience do not seem to belong to the sensory signal itself, but to the efference copy of the motor signal. In our example of the tactile stimulation of the finger, the sense of ownership, and of being the agent (the author) of the sensation, would be referred to the movement of the finger itself rather than to the tactile sensation encountered. This means that in the event that the finger does not move but is instead passively contacting the object due to a displacement of the latter, there could be no sensation, which is however not what we actually do experience in these circumstances.

The issue can be solved, I believe, if we go back to consider the sensory signal for what it is or, better, for what it must have been

originally according to Reid and Humphrey: i.e., a bodily reaction, a movement, an action in itself.

Let's try to explore this idea with a little detail. Essentially, the *Reafferenzprinzip* asserts that an organism can predict the sensory consequence of its own action, that is, the sort of sensory stimulation that should occur as a result of its own movement. Here I would like to consider it the other way around, namely, that an organism can predict the kind of motoric consequence, i.e., of bodily reaction, which should follow from its sensory activity. This is exactly what it should happen, assuming, following Reid and Humphrey, that the sensation is actually a bodily reaction, and therefore ultimately a motor response itself.

In short, I am speculating here that the efference copy which underlies sensation (and thus conscious experience) is the copy of the sensory signal intended as a bodily reaction, and therefore a motoric activity in itself. The double province of the senses alluded by Reid was in a certain way predisposed by the fact that sense organs such as photoreceptors, that respond to light, were originally derived from cilia [25], thus comprising from the start a motoric with a sensory aspect. The distinction became, however, operative only when the motoric component of the sensory signal (the bodily action) started to be used as a signal to compare it with the (ordinary) efference copy associated with active motion. The hypothesis looks plausible because of widespread evidence of centrifugal connections within the sensory systems. For example, in mammals the fibers of the thalamofugal pathway project from the retina to a nucleus of the thalamus, the lateral geniculate body, and from there to the visual cortex. The lateral geniculate body, however, not only receives this information «from below», because the main input to the geniculate actually comes «from above», from the cortex itself and actually constitutes eighty percent of its excitatory afferents. The effect of these synapses is probably inhibited when a signal is generated for an active eye movement.

Consider the phenomenon of blindsight [3], whereby certain patients with primary visual cortex lesions are able to show residual vision capabilities, without these being accompanied by any subjective experience. The enigmatic aspect of blindsight is that patients must be *convinced* that they can see in order to reveal their residual abilities. In fact, they seem to lack the ability to recognize visual activity as their own activity, the sense that seeing belongs to them as something they do, not as something that simply happens to them. The reason, I believe, could be precisely the absence of the massive return input from the cortex to the geniculate, which, under normal conditions, would provide the efference copy of the sensory signal itself, the bodily reaction.

Let's try again with our tactile stimulation example. First case: I move a finger with an active movement and in doing so at a certain moment I come into contact with an object. The immediate result, if I don't focus my attention on the finger, is that there is something out there, the object of my perception. The signal associated with the sensory/bodily reaction occurring on the surface of the finger (or internalized as brain activity) has been sent to a comparator where it becomes annihilated, because a motor corollary signal related to the command for the movement of the finger also reached the comparator. Second case: my finger is still, there is not any active movement of it, but some object has come upon it, stimulating its surface. The immediate result is that something happened on the surface of my finger. The sensory/bodily signal produced by the stimulation has been sent to the comparator, but this time it has not been canceled by any efference copy related to active movement of the finger itself. Now I feel something on my finger, something that happened to me.

In this view, what we call feeling would be nothing more than the outcome of the comparison between the efference copy of the sensory/bodily response and the efference copy of a motor action that may or may not have been already occurred. So, indeed, a memory, as stressed by Godfrey-Smith [20] and Taylor [24], though of a particular kind, for it is actually a memory of a bodily reaction, which carries on with it the sense of having been accomplished (hence the sense of belonging and authorship) and its hedonic value: it is beneficial, I leave my finger there, it is harmful, I move it away …

In sum, once we admit that what appears to be a sensory signal, and the copy of it, is in reality, or was originally, a bodily reaction, the passage of such a signal to the comparison phase (in the absence of a corollary discharge associated with an active movement) leaves the hedonic value to the stimulus (I like it, I don't like it) and the specificity of the response itself. Specificity here refers to the fact that feeling has a precise content, a quality (at this very moment, the green of the garden grass that I look at from the window, the cold of the glass with the iced drink in my hand …). As Humphrey [7,8] noted, these contents are derived, originally, from the type of bodily reactions that stimuli gave rise to in the different districts of the membranes of our ancestors. They are thus contingent, that is, linked to our evolutionary history, but they are not arbitrary.

5. Who is sentient?

Needless to say, I would consider the presence (either peripheral or central) of the mechanism of reafference in organisms with active motion as the signature of sentience. The strategy to route copies of movement commands to sensory structures is widespread and very well studied all across the animal kingdom, from nematodes to primates (see for a review [26]). What about other organisms like protists or plants? In principle, it would not appear impossible to conceive an efference copy mechanism in plants. Although they lack neurons and muscles, movements related to changes in growth or turgor have been described, and it has been claimed that plants are also equipped with some form of movement accuracy mechanism, which adjusts the movement by means of secondary submovements ([27], this issue). However, I am not aware of any evidence of mechanisms disentangling in plants that a source of stimulation is either the outcome of a movement associated with growth/turgor of the plant itself or of something that has simply come into contact with the surface of the plant. Besides, I suspect that if such mechanisms existed the time lapse associated with the operating of the comparator would be exceedingly long due to the time frames of the growth/turgor kind of movements of plants. Given the current heated debate on the status of the so-called « plant neurobiology» (e.g., [28,29]) and the fact that doubts have been raised (see [30]) on even the mere existence of Pavlovian conditioning in plants [31], I believe we should maintain a skeptical stance until more evidence become available.

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