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Vision-for-perception and vision-for-action: Which model is compatible with the available psychophysical and neuropsychological data?

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ABSTRACT

Westwood and Goodale (this issue) review the evidence for distinct visual streams for action and perception. They argue that, on balance, both the neuropsychological and psychophysical data support this distinction. They claim that critical results were either statistically inconclusive (because they consisted of negative evidence) or based on a suspect "calibration" procedure. Finally, they suggest that explanations dismissing the psychophysical evidence for the TVSH are contradicted by the neuropsychological evidence. We disagree with their assessment. 'Negative evidence' is not necessarily inconclusive. Problems raised by mixed evidence are best dealt with by conducting meta-analytical studies, which so far are only in part consistent with the TVSH. Correction ("calibration") of illusion effects is critical for comparisons across stimuli, studies, and tasks. We furthermore argue that both psychophysical and neuropsychological evidence can be explained without assuming divergent pathways for perception and action.

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1. Introduction

Fifteen years ago, Milner and Goodale (1995) and Goodale and Milner (1992) proposed that the dorsal-ventral anatomical split of the visual cortex may be interpreted as the substrate of two independent functional modules: vision-for-perception (the ventral pathway) and vision-for-action (the dorsal pathway). This "two-visual-systems" hypothesis (TVSH, often also called the "perception-action" hypothesis) has served our field well, not only for its potential to resolve long-standing controversies such as that between direct and indirect theories of visual perception (see Norman, 2002), but also for its ability to organize a large body of data in neuropsychology, neurophysiology, and psychophysics, and to stimulate novel research in these areas. Over recent years, however, the strong division of labour originally proposed by Milner and Goodale (1995) has received increasing critiques (see Franz & Gegenfurtner, 2008; Rizzolatti & Matelli, 2003; Schenk & McIntosh, 2010; Smeets & Brenner, 2006). In a new review, Westwood and Goodale (this issue) argue that these critiques can be challenged. In particular, they propose that a careful analysis of the available data still provides converging evidence for the TVSH. We disagree. Although the TVSH remains useful as a broad characterization of visual functional specializations, we propose that an

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alternative view emphasizing the integration of information across multiple visual modules and brain areas provides a better account of both the neuropsychological and the psychophysical evidence.

In accordance with what we construe as the basic structure of the argument set forth by Westwood and Goodale, our reply is structured into two main parts. In the first (Section 2), we tackle what has proven to be the most controversial aspect of the TVSH, namely, the interpretation of psychophysical evidence on motor and perceptual responses to visual illusions and on related grasping paradigms. Although they acknowledge the controversy, Westwood and Goodale suggest that on balance the evidence from psychophysics is still in favour of the TVSH. However, we are not convinced by their arguments. In the second part (Section 3), we examine their charge that critics evaluated the psychophysical evidence in isolation without paying proper regard to the neuropsychological evidence for the TVSH. They argue that such a practice leads to claims that are contradicted by the neuropsychological findings. We argue that there is no contradiction and that the neuropsychological findings can be explained without assuming divergent pathways for perception and action. In our last Section 4, we discuss Westwood and Goodale's claim that, on balance, the evidence still supports the TVSH. Although it is possible to construct a version of the TVSH that is compatible with the available evidence, such a version is weak and essentially indistinguishable from more conventional views assuming that visual information is processed by multiple modules, combined across the visual cortex, and shared between behavioural tasks.

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2. Psychophysical evidence for the TVSH: are the problems an illusion?

No single aspect of the TVSH has proven more controversial than the interpretation of psychophysical evidence on reported dissociations between perception and action in healthy participants. Fifteen years ago, Aglioti, DeSouza, and Goodale (1995) reported that the size representation used to guide grasping is immune to the Ebbinghaus–Titchener illusion ("size-contrast illusions deceive the eye but not the hand"). This finding was questioned soon thereafter (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnc, 1999), and a flurry of experiments ensued. A simple search for the keywords "perception action illusions" on PubMed returns more than 200 papers, a fact that bears witness to the heuristic value of the TVSH, but also to the difficulties in devising a conclusive test of the claim. Yet, Westwood and Goodale claim that this literature supports the TVSH.

To support this claim, Westwood and Goodale offer four arguments. First, they point out that the failure to replicate earlier reported differences for dissociable effects of illusions on perception and action cannot be regarded as strong evidence against the TVSH. Second, Westwood and Goodale argue that not all studies on illusions and action are equally convincing. In their view, some studies avoid most of the methodological pitfalls identified by critics and still provide unequivocal evidence in favour of their hypothesis. Third, Westwood and Goodale take issue with a correction method employed in some studies that did not support the TVSH's view on visual illusions (Bruno & Franz, 2009; Franz, 2003; Franz & Gegenfurtner, 2008). Fourth, Westwood and Goodale point to new psychophysical evidence suggesting that visual information used for action but not perception may violate Weber's law (Ganel, Chajut, & Algom, 2008). Our points of disagreement are discussed in the following four sections.

2.1. The scientific role of negative evidence

Several psychophysical studies comparing perception and action in healthy participants have revealed performance seemingly consistent with visuomotor mechanisms operating independently of conscious perception. However, in many of these studies the reported dissociation between the motor and the perceptual response has been shown to be more apparent than real (for recent reviews see: Bruno, Bernardis, & Gentilucci, 2008; Franz & Gegenfurtner, 2008; Schenk & McIntosh, 2010; Smeets & Brenner, 2006). For example, analyses of the Aglioti size-contrast paradigm have shown that the paradigm itself tended to produce the dissociation, as the perceptual task was not matched to the motor task (Franz et al., 2000; Pavani et al., 1999, see below). Similarly, a number of studies have reported that delaying a grasp causes a shift from dorsal to ventral control (e.g., Hu & Goodale, 2000; Westwood & Goodale, 2003; Westwood, McEachern, & Roy, 2001). However, Franz, Hesse, and Kollath (2009), using the Müller-Lyer illusion, found that the critical factor in modulating the accuracy of the grasp is not a shift from dorsal to ventral control, but the availability of visual feedback.

In their review, Westwood and Goodale acknowledge that some of the psychophysical findings in support of the TVSH do no longer appear as compelling as previously thought, but they claim that some of the critical reports are less damaging to the TVSH than the critics seem to think. First, they point out that the failure to demonstrate a clear distinction between action and perception in a particular task or situation can never be taken as strong evidence against the TVSH. This is a reasonable statement, but it does not provide a compelling response to some of the specific studies that were used to challenge the TVSH. For example, Franz, Fahle, Bült-

hoff, and Gegenfurtner (2001) studied the effect of the Ebbinghaus illusion on size perception and grasping. Franz and his colleagues used the very same illusion and task that were first employed in the pioneering study by Aglioti et al., and did not just report a failed replication of the Aglioti et al. study. Instead, they undertook a detailed study to explore whether purely methodological reasons can account for the reduced effect of illusions on action. One significant methodological problem of the Aglioti study relates to the way in which the effect of the illusion was measured in the perceptual as compared to the grasping task. Franz and colleagues showed that these procedures led to an overestimation of the illusory effect in the perceptual task. They went on to show that if comparable procedures are used, the effects of illusions on perception and grasping are no longer different. This is not simply a failure to replicate earlier results, it is a demonstration that the earlier findings may be due to methodological artifacts. This is not enough to disprove the TVSH, but we believe it is enough to discount evidence which has been and is still cited as strong evidence in favour of the TVSH.

Next, consider the second reason cited by Westwood and Goodale to explain why negative findings on visual illusions are not damaging to the TVSH. Westwood and Goodale claim that "studies that fail to find a difference ... are difficult to interpret for all the same reasons that make it difficult to argue in favour of a statistical null hypothesis." In our view this statement is problematic. Studies that failed to find a difference did not base their conclusions solely on the non-significant difference between the perceptual and action tasks. They also showed that visual illusions had a significant effect on action. This latter finding rules out a strong version of the TVSH, i.e. a version which claims that visually-guided actions always bypass the content of conscious perception. It does not rule out a weaker version which acknowledges that the content of conscious perception will sometimes affect action, but that its impact on action is less pronounced (for a further discussion of the difference between the strong and weak version of the TVSH, see Section 4). To support the weak version it is sufficient to demonstrate that action is less affected by visual illusions than perception. In the context of this version the argument by Westwood and Goodale has more force, but it also creates another problem: It becomes necessary to test the difference between two dependent variables. We will argue below (Section 2.3), that this can only be done if the two variables are made comparable by using a correction procedure ("calibration"). It appears to us that by criticizing this procedure, Westwood and Goodale undermine the methodological basis of testing perception-action differences.

However, in this section we focus on the problem of interpreting null-results. It appears that the weak version of the TVSH can only be challenged by demonstrating that no difference between perception and action exists, but such a demonstration seems problematic since it affirms the null-hypothesis. Is it, therefore, possible to challenge the weak version? The answer clearly depends on our response to two questions: How weak is the weak version, and, is it true that confirming the null-hypothesis is uninformative under any circumstances? If it is merely claimed that action may occasionally be a little bit less affected by certain visual illusions than perception, a weak TVSH will be almost impossible to disprove. But such a hypothesis will not only be difficult to test, it will also have little predictive power and will thus be quite uninteresting. Thus, we have to assume that the weak version means more, namely that certain visual illusions as, for example, the Ebbinghaus illusion will in most cases have a substantially larger effect on perception than on action. In this case we should expect a substantial difference between perception and action in most relevant studies. But if many studies did not produce such a difference, simply ruling out these findings as inconclusive becomes increasingly problematic.

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