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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 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, Bülthoff, 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.

Our line of reasoning is in fact standard practise in all natural sciences, although somewhat underutilized in psychology (cf. Meehl, 1967). With adequate statistical power and sufficiently precise measures, it is quite possible to argue that a set of observations is not different from a theoretical expectation (e.g., Cohen, 1994; Gigerenzer, 1993; Kline, 2004; Loftus, 1996).

Moreover, we cannot fail to notice that Goodale and colleagues are considerably less dismissive of null-results when these support the TVSH. Hu and Goodale (2000) argued for a perception–action dissociation because they found an effect on perception but no significant effect on action. In this study it was not tested whether the difference between the two measures was significant and a later re-analysis by Franz and Gegenfurtner (2008) showed that this difference was indeed far from reaching the level of significance. A similar reliance on null-results can be found in many other studies supporting the TVSH both from the psychophysical and neuropsychological literature (e.g. Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991; Rice, McIntosh, Schindler, Démonet, & Milner, 2006). To sum up, we do not wish to endorse the practise of relying on null-results in all of the above cases, but it is clear that null-results should be taken seriously if they have been obtained under appropriate conditions.

2.2. Meta-analysis provides a more objective way to make sense out of mixed data

A balanced evaluation of a literature as complex as the psychophysics of perception and action requires integrating studies after careful evaluation of differences in methodological details and after applying appropriate corrections to make the data comparable. Such corrections will for example compensate for differences in the employed stimulus-sizes and differences between the slopes of the grasp-size function (for more details, see Bruno et al., 2008). This in turn requires going beyond the logic of individual null-hypotheses, in favour of approaches that stress replication rather than exclusion of "negative" results. Meta-analytical techniques provide the appropriate tools for this endeavor, and so far meta-analytical attempts at making sense of psychophysical comparisons between perception and action in specific domains have not provided clear support for the TVSH.

Given that Westwood and Goodale focus on grasping data, the relevant papers are that of Franz and Gegenfurtner (2008) on the Ebbinghaus–Titchener illusion data, and that of Bruno and Franz (2009) on the Müller-Lyer illusion data. These two papers converge in showing that, when considering effects across different studies, these literatures are not as contradictory as they seem if one simply looks at the outcomes of individual null-hypothesis tests. Rather, they converge in indicating that grasping (i) is never fully immune from illusions; (ii) is less affected by illusions than perception if performed under full visual guidance, thereby allowing the use visual feedback (closed-loop grasping); but (iii) is affected by the illusion as much as perception whenever the grasp is performed without visual feedback (open-loop grasping, both with and without delay). This is not to say that we can now draw a final conclusion against the TVSH. There may be other critical factors that we do not yet understand, and there are indeed other psychophysical tasks besides those on illusions where the available data are too limited to perform a meaningful meta-analysis.

In addition, it should be stressed that another meta-analysis on rapid pointing on the Müller-Lyer illlusion (Bruno et al., 2008) yielded results more in line with the TVSH. Again, this may be due to factors that are still not well understood, or to a fundamental difference between the visual guidance of grasping and rapid pointing. As a theoretical discussion of potential differences between grasping and other motor responses is beyond the scope of this reply (but see also Bruno, Knox, & de Grave, 2010), we will conclude by simply acknowledging that further research is needed. Before we move on to the next issue, however, a final point should be noted. Critical to any meta-analysis is the computation of comparable effect sizes for individual studies, and one crucial aspect of such a computation requires correcting the raw effects by the scaling of the response, motor or perceptual, to the underlying physical variable. Westwood and Goodale refer to this correction as "calibration" (as suggested by a talk of Franz (2010)) and have argued that its use is problematic. If correct, this point would represent a serious problem for meta-analysis. We address this issue in the following subsection.

2.3. Is calibration problematic?

Westwood and Goodale question the rationale for using corrected rather than raw illusion effects when comparing perception and action tasks (e.g., Bruno & Franz, 2009; Franz, 2003; Franz et al., 2001). This is surprising given that researchers across all theoretical orientations have utilized and described this as a valid approach. For example, Dewar and Carey (2006) explained in detail the rationale for using corrected effects and used them to support the TVSH. Similarly, Glover and Dixon (2002) used exactly the same rationale to calculate what they called "scaled illusion effects" and used them to criticize the TVSH.

In these and other papers, a correction was used because different dependent measures typically respond in different ways to the information specifying changes in physical object size. Consider the basic comparison between the maximum grip aperture (MGA) in grasping (the "action" measure) and the finger aperture in manual estimation (the "perception" measure). The scaling of these dependent measures to physical size varies somewhat across studies, but there is consensus that the MGA for closed-loop grasping is a linear function of size with a slope of about 0.8 (Jeannerod, 1981; Smeets & Brenner, 1999). That is, if the size of the object is increased by 1 mm, then MGA will on average be increased by 0.8 mm. The finger aperture in manual estimation, however, yields slopes that can be twice as big. For instance, Franz (2003) found a slope of approximately 1.6 for manual estimation. Similarly, Haffenden, Schiff, and Goodale (2001) found for grasping slopes "that were only half the magnitude of those shown in manual estimation" (pp. 179–180). This difference, consistently found in many laboratories, has important implications for the measure of the illusion effect.

To see this, suppose we introduced an illusory context, and found that the illusion caused the dependent measures to differ by, say, 1.6 mm in the estimation task and by 0.8 mm in the grasping task. By considering only these raw illusion effects, one would be led to conclude that the illusion effect on perception was twice as big as the illusion effect on action – a "dissociation" between perception and action. But note that the perception–action difference is entirely due to the different scaling of the two measures to physical object size. In the estimation task, a 1.6 mm difference corresponds to a change in physical size of 1 mm. In the grasping task, a 0.8 mm difference corresponds to a physical change of 1 mm. Thus, the seeming dissociation is simply a difference in the response to object size in the processes that convert the input signal into a response. This is the whole rationale for the correction, which is consistent with what in statistics and metrology is called calibration and is used in all areas of the natural sciences. By dividing the raw illusion effect by the slope of the linear function relating physical size to the dependent variable, we are defining a common unit for the two measures thereby making them comparable (cf. Fig. 1).

Westwood and Goodale argue that—because the procedure uses the response to physical size to calibrate the effect of the illusion – it mixes two qualitatively different signals (change in physical size

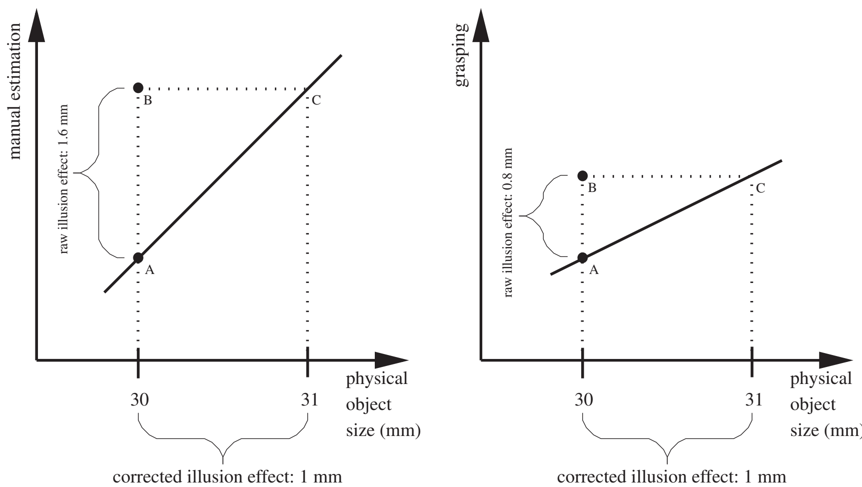

Fig. 1. Calibration procedure. Consider a typical manual estimation task that depends linearly on physical object size with a slope of 1.6 (black line on left panel). Consider an object of size 30 mm that leads to response A if there are no illusion inducing elements. If enlarging illusion elements are introduced and if manual estimation is affected by the illusion, this will lead to a different response, B, which we assume in our example to be 1.6 mm above A ("raw illusion effect"). To evaluate how big the effect of the illusion is, we search for a change in physical size that has the same effect as the illusion. This is point C, which tells us that we need to increase physical size by 1 mm to create the same effect as the illusion. Therefore, the illusion corresponds to a 1 mm increase in physical size ("corrected illusion effect"). Now consider grasping that is also related linearly to physical size but typically with a slope of only 0.8 (black line on right panel). Again, we measure response A and then introduce illusion elements that lead to response B that we assume to be 0.8 mm above A ("raw illusion effect"). Although this raw illusion effect seems smaller than that in manual estimation, point C tells us that the illusion again corresponds to a 1 mm increase in physical size ("corrected illusion effect"), such that the influence of the illusion is in fact identical. Mathematically, the corrected illusion effect is calculated by dividing each raw illusion effect by the slope of the corresponding linear function.

vs. illusory change). They argue that this makes the procedure problematic. However, this argument is inconsistent with the logic of their own experiments because their experiments are also based on the assumption that a change in physical size can be compared to an illusory change of size. For example, consider the Aglioti nulling-procedure: A pair of discs was selected that was perceived under the illusion as being equal in size (e.g., 30 mm and 32 mm in diameter). This pair was then presented for grasping and the question was whether the difference in physical size would be counteracted by the illusion. Assuming under the null hypothesis that grasping is affected by the illusion to the same extent as perception, one would expect that the two discs are grasped with the same MGA. However, this is not what Aglioti et al. found. They found that the MGA differed for the two discs, although they were perceived as being equal in size. Accordingly, Aglioti et al. rejected the null hypothesis and concluded that there is a surprising, new behaviour in grasping that deviates from the a priori to be expected behavior.[1] Now here is the critical point: This null-hypothesis rests on the assumption that the effect of a difference in physical size (30 mm vs. 32 mm) can be compared quantitatively to the effect of the illusion. Otherwise it would not make sense to expect the illusion to counteract the difference in physical size in grasping. This is exactly the assumption that is criticized by Westwood and Goodale with respect to the correction procedure. The only difference is that while Aglioti, Goodale and colleagues implicitly assumed identical response functions for grasping and perception in their experiments, the correction procedure does not make this additional assumption. Therefore, the correction procedure in fact relies on *less* assumptions than the experimental designs used by Goodale and colleagues. In short, we believe that correction (or calibration) of illusion effects is indispensable, if meaningful comparisons are to be made across different perceptual and motor tasks as well as across studies in meta-analysis (see Section 2.2 above).

Westwood and Goodale also make a series of accessory claims, which we will now examine in detail. We agree with Westwood and Goodale that the correction will not change the results of all studies. If in a study the slopes of the different response measures are not different then, of course, the correction will not make a difference. For example, the slope of manual estimation seems to only be different from grasping if the hand cannot be seen during manual estimation. For example, Dewar and Carey (2006) found under full vision conditions similar slopes for grasping and manual estimation. However, in some studies that used manual estimation (e.g., Haffenden & Goodale, 1998) the slopes were clearly different, and therefore corrections do make a big difference.

We also agree that, in principle, it may be useful to take into account other aspects of the displays when correcting illusion effects. For instance, luminance has been shown to affect perceived 3D structure and may therefore indirectly affect perceived size (Dosher, Sperling, & Wurst, 1986). This would not undermine the logic of the correction but simply make it more accurate by controlling another potential component of observed raw effects.

Westwood and Goodale also cite a study by Ganel, Tanzer, and Goodale (2008) as evidence that there are results which will hold up regardless of whether a correction procedure is used or not: By arranging the stimulus sizes in a special way, Ganel, Tanzer, et al. (2008) created for the Ponzo illusion a situation where the size indicated by the perceptual measure was opposite to that found in the grasping measure. This was achieved by using a smaller physical size in the illusory enlarging part of the Ponzo figure than in the illusory shrinking part and by choosing this physical size difference such that it was large enough to counteract the illusion in grasping but not in perception. In other words, Ganel, Tanzer, et al. (2008) observed a larger illusion effect in perception than in grasping. Westwood and Goodale correctly point out that the correction procedure would not have changed this result. However, this does not undermine the logic of the correction procedure. It merely shows that the failure to use an appropriate correction cannot be the only reason why visual illusion sometimes have a stron-

[1] To avoid confusion, a comment might be necessary here: We are only interested in the mathematical structure of Aglioti et al.'s reasoning here because we want to demonstrate that they use assumptions that Westwood and Goodale critizise with respect to our correction procedure. The fact that we are skeptical about the conclusions of Aglioti et al.'s study is based on the finding that their tasks were not well matched (Haffenden et al., 2001), which is a different topic.

ger effect on perception than action. Time will show whether the true reason for this difference is a functional dissociation between perception and action as suggested by Westwood and Goodale. One important point in this respect is that, in the main experiment of this study, grasping was performed under full vision of the hand, such that visual feedback will likely have reduced the illusion effect (see below and Bruno & Franz 2009). Although Ganel, Tanzer, et al. (2008) reported a control experiment aimed at addressing this problem, their control experiment could not fully rule out this possiblity. This is so because in this control experiment vision was prevented at movement onset but reinstalled towards the end of each grasping movement, such that participants might have calibrated their grasps to the true object size across trials. In fact, in the case of saccades, there is evidence that providing target information at the end of the movement helps to recalibrate the following saccades (Bruno, deGrave & Knox, 2010).

To sum up: The correction procedure is needed. Its logic is neither undermined by the theoretical arguments nor by the empirical examples provided by Westwood and Goodale. When the procedure is applied consistently, a substantial erosion of the evidence base for the TVSH is observed.

2.4. Do actions violate fundamental psychophysical principles?

In two recent papers (Ganel, Chajut, Tanzer, & Algom, 2008; Ganel, Chajut, & Algom, 2008), Ganel and his colleagues studied the precision of visually-based size representations in different grasping and perceptual tasks. In the perception tasks, they found that the differential threshold (JND) increased with the size of the judged object. This is in accordance with the fundamental principle of perception known as Weber's law: in any given sensory channel, the JND is a constant fraction of the reference stimulus intensity, such that the JND for a larger object should be larger than the JND for a smaller object (and hence the precision of the perceptual judgments should be small in the first case and bigger in the second case). In contrast with what happens in perception data, however, Ganel and colleagues reported that JND's for visuomotor size representations (as measured by the standard deviation of the MGA) did not increase with object size but remained approximately constant. Thus they concluded that grasping violates a fundamental psychophysical principle.

Westwood and Goodale point out that, if this interpretation were confirmed, this finding may represent an important piece of evidence that vision-for-action operates on a fundamentally different representation of size than vision-for-perception. Given the potential importance of the result, however, it is important to understand exactly what is the nature of the supporting data. Ganel and colleagues reported three grasping experiments. The first two were closed-loop grasps ("grasping" and "real-time grasping" conditions in Ganel, Chajut, & Algom, 2008). In these conditions, vision of the hand and of the target during the action allows participants to perform on-line corrections while they guide the hand to the object. The important point here is that this form of online correction is available only in the grasping condition and not in the perceptual condition. This means that in the action-condition, initial errors in the estimation of the object's size can be later corrected on the basis of visual feedback. However, the same is not true for the perceptual condition, where the initial estimation-error will find its way without correction into the perceptual report. In this situation, where grasping is carried out under a closed-loop condition, it is therefore not surprising, that the distribution of errors is different for perception and action. A violation of Weber's law in these conditions is therefore fully consistent with earlier proposals that actions dissociate from perception only in closed-loop conditions (see, for instance, the "motor control" hypothesis of Bruno & Franz, 2009). In the third experiment, however, this account does not apply as it involved open-loop grasping ("real-time movement programming" condition in Ganel, Chajut, Tanzer, et al., 2008). The result of this third experiment is challenging, and it deserves close scrutiny. However, we will wait for replications and extensions before being convinced that actions violate Weber's law.

3. Is the TVSH required for a unified account of the psychophysical and neuropsychological data?

In Section 2, we examined Westwood and Goodale's assessment of the psychophysical evidence in support of TVSH and found their arguments unconvincing. However, Westwood and Goodale also argue that the psychophysical evidence should not be evaluated in isolation, because such an isolated critical discussion leads to claims which are contradicted by the neuropsychological evidence. In particular, they suggest that data from DF have already disconfirmed the idea of a common visual representation for perception and action. Hence, they imply, some version of the TVSH is needed for a unified account of the psychophysics and neuropsychology of perception and action. But is this really the case?

Let us first state our point of agreement. We agree with Westwood and Goodale that the neurological evidence, in DF and in other patients, is not consistent with the proposal that all visual processes fuse into one, single visual representation that forms the only basis for all visually-guided behaviour. However, we should not overlook that this is not the only alternative to the TVSH.

Another alternative is to propose that numerous visual processes are operating in parallel, involving a variety of ventral and dorsal circuits. These processes can provide visual information to constrain both perceptual decisions and visually-guided actions, but do not have to be necessarily fused into one unified representation (for relevant physiological evidence, see Nelissen et al., 2009; Orban, 2011; for a similar suggestion in the philosophy of mind, see Dennett 1991). Such a view could explain the perception–action dissociations observed in DF (see also Schenk, 2010, for a more in depth analysis of this argument).

The key point here is that the environment is rich in visual information that can be employed to guide actions. For example, in reaching for a target we can use either binocular, extraretinal or monocular cues to assess a target's distance. Not all of those visual cues are needed to make a successful reach and it is therefore not surprising that DF will succeed even if access to some of the cues (e.g. the monocular cues) is lost. But this does not mean that healthy subjects will also disregard monocular cues when they reach for a target. For instance, it has been demonstrated that familiar size – which is unavailable to DF – is used in healthy subjects in conjunction with binocular cues to guide their reaching and grasping movements (McIntosh & Lashley, 2008). This suggests that the visuomotor process in a patient with ventral stream damage may not be the best model for the normal visuomotor process. Most importantly, this suggests that sharing of information across the two streams may be the rule rather than the exception in the healthy visual system, a view that accounts nicely for the psychophysical results as well.

In our view this means, that the TVSH is not necessary to jointly account for the psychophysical and neuropsychological findings. But, one might still argue, even if the TVSH is not logically necessary it nevertheless provides the most plausible account for the available evidence. However, in our view the real question is not whether the TVSH can provide a plausible account but *which* version of the TVSH can do so. Since its inception the TVSH has undergone changes. Early versions of the model emphasized two streams that are separate both anatomically and functionally. It was proposed that action programming relies on dorsal information and ventral input is only used when actions are delayed or when visual information is used for of action planning (see for example, Milner & Goodale, 1995, 2006, 2008). Similarly, visual illusions were assumed to have hardly any effect on actions (see for example, Aglioti et al., 1995).

In the version of the TVSH presented in their recent review, Westwood and Goodale describe a division of labour with a much higher degree of flexibility. The distinction between action programming and planning, which is conceptually and empirically difficult to maintain (Schenk, 2010), is no longer mentioned. Instead it is acknowledged that whether the ventral stream is involved in the visual guidance on action depends on the visual information that is required and available for a given visuomotor task. In particular, it is acknowledged that the ventral stream processes a specific type of spatial information (e.g. monocular cues). When such information is required in a motor task, the ventral stream then becomes involved – a position not so different from the view proposed by Smeets and Brenner (1995) and Schenk (2006). But this implies that the ventral stream is not just there for perception and that the dorsal stream is not the exclusive repository of visual information for action guidance.

The position on illusion has also shifted from the claim that visual illusions have hardly any effect on action to a position which emphasizes that the effects of illusions on action are less than those on perception. But what are the implications of such a shift in terms of the respective contribution of the ventral and dorsal streams to action guidance? It means that both ventral and dorsal stream areas typically provide visual information for the guidance of action but the weighting of the ventral stream's input in action tasks may be typically less than its weighting in perceptual tasks. We believe that such a position is not necessarily controversial. However, it is also not very surprising. If we take into account the fact that visuomotor tasks often include relevant sensory information (e.g. visual feedback, haptic feedback from the target object) which is either not available or not relevant for success in the perceptual task, it is to be expected that the influence of the purely ventral stream input will become diluted. However, we would also like to emphasize that there are now quite a number of instances where the illusory effect on action is indistinguishable from that on perception. Thus, if we take the effect of illusions as indicator of ventral stream involvement, a position which remains controversial (see Murray, Boyaci, & Kersten, 2006), we are left with the insight that the weighting of the contribution of ventral stream information is sometimes but not always less than that for dorsal stream input.

After these changes, one might justifiably ask whether the proposal should still be dubbed a two-visual-systems hypothesis. What sets it apart from other views of the visual cortex? Two reviewers of this reply suggested that the TVSH is different from earlier and alternative views of visual function because it proposes that the dorsal stream is specialized for visuomotor control. However, both proponents and opponents of the TVSH accept that visual neurons in the parietal lobe seem to be intimately linked with visuomotor tasks. In fact the insight that the posterior parietal cortex plays an important role in the visual guidance of action predates the TVSH by approximately 20 years (Haaxma & Kuypers 1975; Hyvärinen & Poranen 1974; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuña, 1975; Rondot, De Recondo, & Ribadeau Dumas, 1977; Faugier-Grimaud, Frenois, & Stein, 1978; Stein 1978). It is true that the proponents of the TVSH elaborated further on the dorsal streams role in action guidance. But it also true that some of those elaborations have proved quite controversial (Husain & Nachev 2006; Rizzolatti & Matelli 2003; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Schenk & Milner 2006). Nonetheless, an important and enduring feature of the TVSH is the insistence that visual processes are shaped by the behavioural task. In our view this is an important insight. It is an insight that we endorse and that we believe will continue to inspire future research.

4. Conclusions

In their review of the literature on the TVSH, Westwood and Goodale find that there is still good support for their notion of encapsulated vision-for-action and vision-for-perception modules. For many of us who followed and contributed to recent critical reappraisals of the relevant evidence (see for example Schenk & McIntosh, 2010), this conclusion is surprising. As we have argued in this reply, a number of individual results and meta-analyses now provide evidence that actions can be affected by contextual illusions in conditions whereby the TVSH predicts that they should not. We have also argued that these results cannot be disregarded as inconclusive failures to reject statistical null hypotheses, or underplayed in favour of other results that are more in line with the TVSH. Furthermore, we argued that it is unnecessary to assume diverging pathways for perception and action in order to account for the neuropsychological findings. No doubt, some version of the TVSH can be made compatible with the available evidence, but it should be acknowledged that such a version would not differ much from a view that emphasizes the sharing of visual information across pathways and functions. But there is common ground between us and Westwood and Goodale. We both agree that the way information is used and processed in the visual brain will be shaped by the behavioural task. Uncovering the precise details of how this happens should be the common aim of our future research.

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