



Research report

Functional dissociation between action and perception of object shape in developmental visual object agnosia

Erez Freud ^{a,*}, Tzvi Ganel ^a, Galia Avidan ^a and Sharon Gilaie-Dotan ^{b,**}

^a Ben-Gurion University of the Negev, Beer-Sheva, Israel

^b UCL Institute of Cognitive Neuroscience, London, UK

ARTICLE INFO

Article history:

Received 18 August 2015

Reviewed 6 October 2015

Revised 27 October 2015

Accepted 18 December 2015

Action editor Rob McIntosh

Published online 7 January 2016

Keywords:

Two visual systems

Action-perception

Grasping

Visuomotor control

Efron blocks

ABSTRACT

According to the two visual systems model, the cortical visual system is segregated into a ventral pathway mediating object recognition, and a dorsal pathway mediating visuomotor control. In the present study we examined whether the visual control of action could develop normally even when visual perceptual abilities are compromised from early childhood onward. Using his fingers, LG, an individual with a rare developmental visual object agnosia, manually estimated (perceptual condition) the width of blocks that varied in width and length (but not in overall size), or simply picked them up across their width (grasping condition). LG's perceptual sensitivity to target width was profoundly impaired in the manual estimation task compared to matched controls. In contrast, the sensitivity to object shape during grasping, as measured by maximum grip aperture (MGA), the time to reach the MGA, the reaction time and the total movement time were all normal in LG. Further analysis, however, revealed that LG's sensitivity to object shape during grasping emerged at a later time stage during the movement compared to controls. Taken together, these results demonstrate a dissociation between action and perception of object shape, and also point to a distinction between different stages of the grasping movement, namely planning versus online control. Moreover, the present study implies that visuomotor abilities can develop normally even when perceptual abilities developed in a profoundly impaired fashion.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

One of the most influential models regarding the organization of the cortical visual system proposes a segregation between a ventral pathway, which mediates object recognition, and a

dorsal pathway, which supports spatial representations (Ungerleider & Mishkin, 1982) and goal-directed actions (Goodale & Milner, 1992). Consistent with this division of labor, many behavioral studies, with healthy adults as well as with neuropsychological patients, have demonstrated a functional dissociation between vision-for-action and vision-

* Corresponding author. Postal address: Department of Psychology, Ben-Gurion University of the Negev, Beer-Sheva, Israel.

** Corresponding author. Postal address: UCL Institute of Cognitive Neuroscience, 17 Queen Square, London WC1N 3AR, UK.

E-mail addresses: erezfreud@gmail.com (E. Freud), shagido@gmail.com (S. Gilaie-Dotan).

<http://dx.doi.org/10.1016/j.cortex.2015.12.006>

0010-9452/© 2016 Elsevier Ltd. All rights reserved.

for-perception (for a recent review see Goodale, 2014, but see Glover & Dixon, 2001; Himmelbach & Karnath, 2005; Schenk & McIntosh, 2010 for critics and alternative models). Additionally, neuroimaging and electrophysiological studies, in human and non-human primates, further demonstrate the involvement of occipitoparietal regions in visually-guided actions while occipitotemporal regions are involved in mediating object perception (for a recent review see Gallivan & Culham, 2015).

Nevertheless, it is unclear whether normal emergence of each of these two predominantly separated functional networks depends on normal development of the visual system, or whether one functional network could normally emerge even when the other does not due to abnormal visual system development from early childhood or even from birth. This question is particularly of interest given the rich anatomical and functional connections between the ventral and dorsal pathways (Himmelbach & Karnath, 2005; van Polanen & Davare, 2015; Yeatman et al., 2014). In the present study, we examined this question in the context of object shape representation and asked whether the vision-for-action system, which is presumably mediated by the dorsal pathway, could develop normally even when the vision-for-perception system, presumably mediated by the ventral pathway, was compromised from an early age.

Only a few studies have examined the developmental association between the vision-for-action and vision-for-perception systems and these yielded mixed results. For example, Hadad and colleagues have found that similarly to adults (Ganel, Chajut, & Algom, 2008; Ganel, Freud, & Meiran, 2014, but see Smeets & Brenner, 2008; Utz, Hesse, Aschenneller, & Schenk, 2015 for critics), children at the age of five show a dissociation between action and perception (Hadad, Avidan, & Ganel, 2012). In particular, like adults, children adhere to Weber's law (Stevens, 1975) in a perceptual task but not in a grasping task. On the other hand, Schum, Franz, Jovanovic, and Schwarzer (2012) utilized the Garner speeded classification task to show that in childhood, both action and perception rely on integral processing of the stimulus (i.e., processing the object as a whole) while in adulthood, action relies on analytical processing of the stimulus (i.e., piecemeal processing of a given dimension) whereas perception relies on integral processing (Ganel & Goodale, 2003).

These inconsistencies were also reflected in a study that examined children's sensitivity to the Ebbinghaus illusion in perceptual and grasping tasks. In particular, similarly to adults, children were affected by the illusion in the perceptual task but during grasping, the illusory effect on their motor control was in a direction opposite to that of adults and to their own perceptual effect (i.e., discs of the same size were grasped with a smaller aperture when surrounded by small distractors, while perceived as being larger; Hanisch, Konczak, & Dohle, 2001).

The development of a neurofunctional dissociation between the two pathways was examined in a neuroimaging study in congenitally blind human adults. In that study, "visual" stimuli were presented via audition by means of a sensory substitution device while participants performed "visual" localization ("where") or identification ("what") tasks.

The results revealed that in the congenitally blind, similar to the neurotypical controls, regions within the dorsal 'visual' pathway showed higher selectivity to the localization ("where") task, while regions along the ventral 'visual' pathway showed higher selectivity to the identification ("what") task. While that study focused on a "Where/What" distinction (Ungerleider & Mishkin, 1982) between the dorsal and ventral pathways rather than on a How/What distinction (Goodale & Milner, 1992), which is the focus of the current investigation, the findings suggest that a neuro-functional dissociation between the dorsal and ventral pathways might be innately wired (Striem-Amit, Dakwar, Reich, & Amedi, 2012).

Visual object agnosia can also provide significant insights about the ventral–dorsal pathways relationship, as this condition mainly affects ventral pathway function. Visual object agnosia refers to a deficit in visual object perception which cannot be attributed to deficits in low-level vision, general loss of knowledge about the object (i.e., auditory/tactile recognition are preserved) or to impaired intelligence (Farah, 1994). Most research on visual object agnosia comes from acquired cases following ventral pathway lesions and has focused on perceptual aspects associated with ventral pathway functions (e.g., Farah, 1994; Moscovitch, Winocur, & Behrmann, 1997). In one patient (DF), however, who acquired visual form agnosia in adulthood following brain damage, visuomotor performance has been extensively studied. Even though DF shows a profound vision-for-perception deficit, she exhibits remarkably intact vision-for-action (e.g., Goodale, Milner, Jakobson, & Carey, 1991; James, Culham, Humphrey, Milner, & Goodale, 2003; Whitwell, Milner, Cavina-Pratesi, Barat, & Goodale, 2015; but see Hesse, Ball & Schenk, 2012; Schenk, 2012 for critics). In addition, a recent study with acquired visual agnosia patients also demonstrated a dissociation between dorsal and ventral visual cortices for perceptual tasks. In particular, preserved sensitivity to object 3D structure was found in the dorsal cortex of these visual agnosia patients, while the sensitivity to this type of information along the ventral cortex was significantly reduced (Freud et al., *in press*). Nevertheless, developmental cases of visual agnosia may offer unique and novel perspective about the nature of the dissociation between action and perception. In particular, if vision-for-action could develop normally, even when vision-for-perception is profoundly impaired, it would suggest that the perception-action dissociation is apparent early in-life and reflects a fundamental organizational principle of the visual system.

To the best of our knowledge, only one case of early acquired object agnosia was investigated in a developmental context of the action and perception dissociation. That case is patient SB, who suffers from object agnosia acquired at the age of 3, after massive bilateral lesions to the ventral pathway and a unilateral lesion to the dorsal pathway (Dijkerman, L  , D  monet, & Milner, 2004; L   et al., 2002; Rice et al., 2006). L   et al. (2002) extensively investigated different visual and cognitive abilities including vision-for-action and concluded that the patient had intact visuomotor control. This conclusion was supported by later studies by Rice et al. (2006) and Dijkerman et al. (2004) who showed that SB exhibited preserved visuomotor abilities. Yet, even given these important

observations, some factors limit the conclusions that can be drawn on the developmental trajectory of the dorsal–ventral dissociation. First, SB suffers from acquired agnosia, and therefore, the development of his visual system until the age of 3 was intact. Moreover, SB suffers from unilateral damage to his parietal cortex which may also modulate the neural response of dorsal cortex in the intact hemisphere (See Konen, Behrmann, Nishimura, & Kastner, 2011). Finally, in Lê et al. (2002), no parallel perceptual control task was used and so it is hard to compare between SB's performance during action and during perception. Rice et al. (2006) did compare between action and perception, but their action task was a reaching task, which is fundamentally different from precision grasping and has been shown to rely on different neural mechanisms (Culham et al., 2003). Lastly, Dijkerman et al. (2004) extensively investigated SB's visuomotor performance, but his results were not compared to those of a matched control group. Taken together, despite the informative insights that SB's case provides, it is not yet clear whether visuomotor control could develop normally even when ventral vision is highly impaired from birth.

In contrast to acquired visual agnosia, developmental visual agnosia is found already in early childhood and occurs without any evident lesion to the visual cortex, and without introducing cortical imbalances-caused lesions. Therefore, it offers a rare opportunity to test whether vision-for-action can develop normally despite profoundly impaired vision-for-perception abilities from early childhood. We examined LG, a 28 year-old male, currently a graduate student, who was diagnosed with developmental object agnosia at an early age after exhibiting symptoms of impaired object and face recognition at the age of 2 years (Ariel & Sadeh, 1996). For example, at that age he was not able to visually recognize his grandparents or to assemble simple puzzles under visual guidance. Full neuropsychological assessment at the age of 8 revealed normal intellectual and social skills, alongside profound object agnosia and prosopagnosia (Ariel & Sadeh, 1996). LG's visual agnosia was further investigated during adulthood in a series of studies (Aviezer, Hassin, & Bentin, 2012; Aviezer, Hassin, Perry, Dudarev, & Bentin, 2012; Brooks, Gilaie-Dotan, Rees, Bentin, & Driver, 2012; Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011; Gilaie-Dotan et al., 2013; Gilaie-Dotan, Perry, Bonne, Malach, & Bentin, 2009; Lev et al., 2015; for a review see Gilaie-Dotan, in press). These studies showed that despite no apparent brain lesion on the MRI scans, his intermediate visual regions (V2/V3) were abnormally deactivated in response to visual input, and selectivity to objects and faces along the ventral pathway was compromised (Gilaie-Dotan et al., 2013; Gilaie-Dotan et al., 2009). Interestingly however, a later study showed that LG has intact perception of biological motion, and normal functional connectivity between his occipitoparietal cortex and his fronto-parietal vision-for-action regions (Gilaie-Dotan et al., 2011). These results may point to a potential developmental dissociation between LG's dorsal-related and ventral-related functions. In line with this assumption, LG reports that he relies on haptic exploration to complement his impaired visual perception, and his visuomotor control on every-day tasks seems to be intact.

To test whether a vision-for-action versus vision-for-perception dissociation is present in LG, we assessed his

sensitivity to object shape in a visuomotor (dorsal) task and in a perceptual (ventral) task. We predicted that LG would exhibit impaired sensitivity to object shape in the perceptual task while his sensitivity to object shape in the visuomotor task would be intact.

2. Methods

2.1. Participants

LG, who is a 28 y.o. right-handed male, and a control group of nine right-handed neurotypical male students with normal or corrected to normal vision from Ben-Gurion University of the Negev (ages 24–30) gave written informed consent before participating in the experiment. The control participants received course credit or 7\$ as compensation for taking part in the experiment. The experimental protocol was approved by the ethics committee of Ben-Gurion University of the Negev and by the Helsinki committee of the Soroka Medical Center.

2.2. Apparatus and stimuli

Participants sat in front of a black tabletop on which the target objects were presented at a viewing distance of approximately 50 cm (see Fig. 1). Target objects were six wooden Efron blocks (Efron, 1969) that were matched for surface area (25 cm²), texture, mass, depth, and color, but varied in width and length. The width of the blocks was the relevant dimension for the grasping/perceptual estimation tasks and ranged from 2.5 to 5 cm in gaps of .5 cm (Fig. 1A).

Computer-controlled PLATO goggles (Translucent Technologies, Toronto, ON) with liquid-crystal shutter lenses were used to control stimulus exposure time and prevent any possible exposure to the stimuli prior to trial onset. Grip scaling and manual estimations were recorded by an Optotrak Certus device (Northern Digital, Waterloo, ON). The apparatus tracked the 3D position of the participant's right index finger, thumb and wrist at a sampling rate of 200 Hz, providing a .1-mm positional accuracy under the specified experimental conditions. This was achieved by tracking three active infra-red light emitting diodes that were connected to the participant's index finger, thumb and wrist, and allowed for complete freedom of movement of the hand and fingers.

2.3. Procedure

All participants performed one block of the manual estimation task and then one block of the grasping task. Participants placed their right index finger and thumb on a start button before the beginning of each trial. In the grasping task, following the opening of the shutter goggles, they were asked to reach out and pick up the Efron block across its width using a natural grasping movement with their index finger and thumb (Fig. 1B). The shutter goggles remained open for additional 1500 msec to allow complete visual feedback during each grasp. In the manual estimation task, participants were asked to estimate the width of the target object from a distance of approximately 50 cm, again using their right index

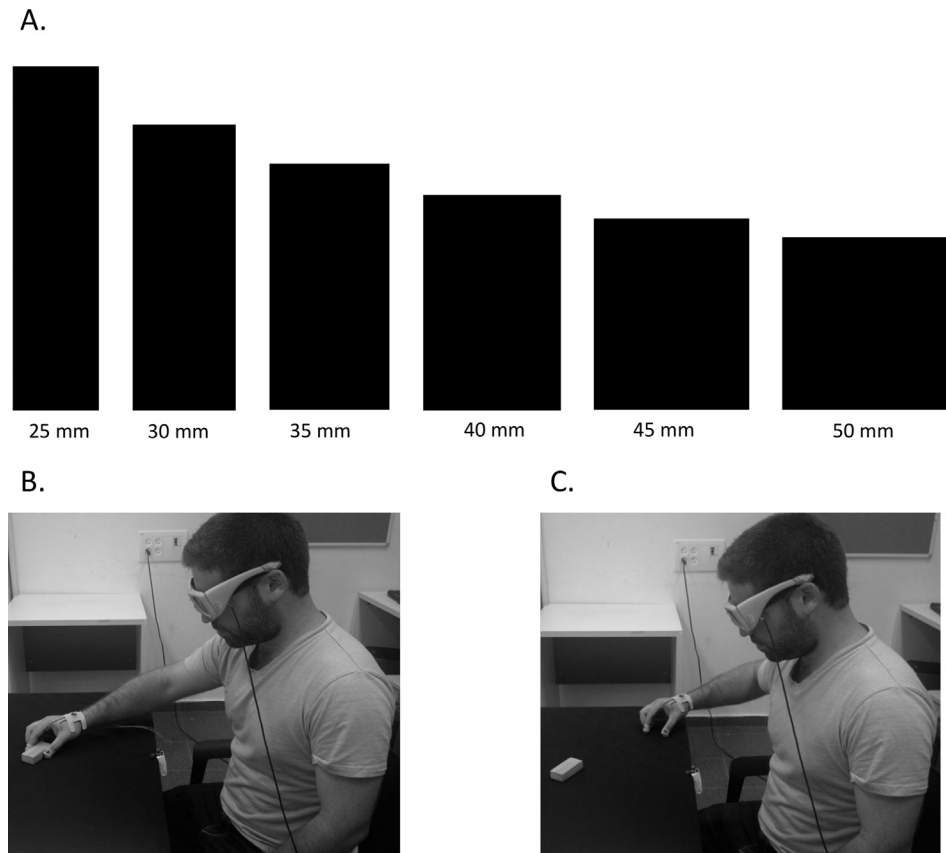


Fig. 1 – Experimental design. (A) The Efron blocks that were used as the experimental stimuli were matched for surface area, texture, mass, depth and color, but varied in width and length (the widths of the blocks are indicated below them). Using their index finger and thumb, participants were asked to **(B)** grasp the block by its width in the grasping task, or **(C)** estimate the width of the object from a distance in the manual (perceptual) size estimation task. (The person in the picture is a lab member.)

finger and thumb (Fig. 1C). To ensure that participants had the same tactile feedback as they did in the grasping task (Schenk, 2012), participants were asked to grasp the object following their manual estimation; the signal to grasp the object was a brief auditory tone presented 1500 msec after the onset of the manual estimation trial.

Experimental blocks began with five practice trials that were excluded from the analysis. In each experimental block, each object was presented ten times in a pseudo-randomized order resulting in a total of 60 trials in the grasping task block, and 60 trials in the manual estimation block.

2.4. Data analysis

The 3D trajectories of the index finger and thumb were recorded. Movement onset (reaction time) was determined as the point in time when the aperture between the index finger and the thumb increased by more than .1 mm for at least 10 successive frames (50 msec). Movement offset was determined as the point in time when the aperture between the index finger and the thumb changed by no more than .2 mm for at least 20 successive frames (100 msec) (Freud & Ganel,

2015). In the manual estimation task, movement offset was determined as the time point in which the tone was presented (1500 msec after trial onset).

To assess sensitivity to the width of the object, we calculated in the case of the grasping condition the relation between object width and hand aperture at the time of the maximum grip aperture (MGA), or the final manual estimation (perceptual condition) by calculating the linear slope of the regression analysis (Goodale et al., 1991). Additionally, to analyze response precision, we computed the Just Noticeable Difference score (JND) for each participant. The JND measures the minimum detectable increment in stimulus magnitude and therefore reflects the sensitivity, which is the size resolution in this case, of the perceptual system of interest (Marks & Algorn, 1998). The JND was calculated based on the within-subject standard deviation of the responses at the point of MGA or the point of the final manual estimation separately for each object width (Ganel et al., 2008).

In the grasping task, we also analyzed other standard kinematic measures of reaction time (i.e., time from trial onset to movement onset), movement time (i.e., time from movement onset to movement offset) and the time taken to reach

MGA. Additionally, to characterize sensitivity to width throughout the movement, we also sampled the grip aperture at 11 normalized time points from movement initiation (defined as 0%) to the final grasping of the object (defined as 100%) in 10% steps, and the grip aperture was calculated for each of these 11 time points. A similar normalization procedure was used in earlier studies (Freud & Ganel, 2015; Ganel, Freud, Chajut, & Algom, 2012) but here we also calculated the slope between object size and grip aperture for each of the segments. To statistically compare between LG and the controls, we first averaged the slopes in each third of the movement (i.e., 10%–30%, 40%–60%, 70%–90%), and then applied the Crawford and Garthwaite's single-case analysis (2002). Lastly, to account for the problem of multiple comparisons, we applied the Bonferroni correction.

3. Results

3.1. Slope

Previous studies (e.g., Goodale et al., 1991; Jeannerod, 1986; Karnath, Rüter, Mandler, & Himmelbach, 2009) have demonstrated a linear relationship between object width and hand aperture, where a slope value of 1 indicates an ideal fit between object width and hand aperture. Following the same procedure as these earlier studies, we calculated the linear slope between these variables in each of the two tasks. The average linear slope between object width and hand aperture in the controls was close to 1 in both the manual estimation and the grasping movement tasks (see Fig. 2A). LG showed a significantly reduced slope in the perceptual task (LG's slope = .64, controls' mean slope = .97), as confirmed by the Crawford and Garthwaite's single-case analysis (2002) [$t(8) = 2.408, p < .05$] (Fig. 2A, right). A different pattern was observed in the grasping task, where LG's slope was well within the normal range [$t(8) < 1$] (Fig. 2A, left). These results suggest that LG has preserved sensitivity to object shape

during visually-guided grasping despite impaired perceptual sensitivity to object shape. Nevertheless, an additional criterion that had to be met in order to adhere to the definition of a classical dissociation between two functions was that the patient's performance on a specific task (i.e., manual estimation) would be significantly poorer compared to their own performance on a different task (i.e., grasping) (Crawford & Garthwaite, 2005). To test this prediction directly, we applied the Revised Standardized Difference Test (RSDT) which measures whether the difference between an individual's standardized score on two conditions (action vs perception) is significantly different from the difference observed in the control sample (Crawford & Garthwaite, 2005). This test showed that LG's performance was significantly worse in the manual estimation task compared to the grasping task [$t(8) = 2.29, p = .05$], thereby demonstrating a classical dissociation between his action and perception of object shape.

3.2. JNDs

The average within-subject variability of responses to each Efron block was used as an additional indicator for sensitivity to their width (Ganel et al., 2008). Here, smaller values reflect finer width resolution. Consistent with the linear slope analysis, LG exhibited normal sensitivity to object shape in the grasping task [$t(8) = 1.01, p > .3$] performing better than 8 of the 9 controls, but was profoundly impaired in the perceptual task, with significantly greater JNDs (poorer perceptual resolution) compared to the controls [$t(8) = 5.034, p < .01$, Fig. 2B]. The RSDT also revealed a significant difference between the two tasks [$t(8) = 3.723, p < .01$], further supporting a classical dissociation between action and perception for object shape in LG.

3.3. LG's visuomotor sensitivity to object shape does not rely on a speed-accuracy tradeoff

The results of the Efron blocks tasks suggest that LG has preserved visuomotor sensitivity to object shape while his

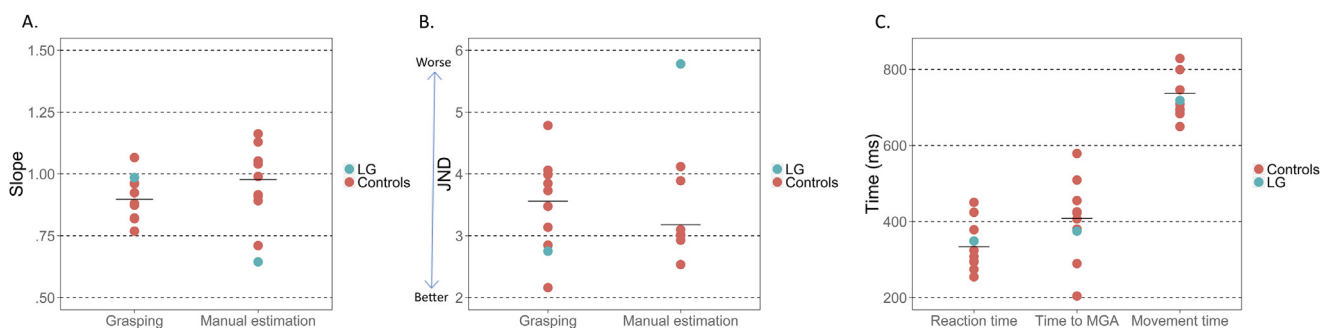


Fig. 2 – Results from the grasping and manual estimation tasks. LG's data is represented by the blue dot, while each of the healthy matched control participants' data ($n = 9$) is represented by a red dot. The mean value of the control group is indicated by a horizontal black line. (A) The linear slope between object width and hand aperture served as an indicator for sensitivity to object width. Values which are closer to one reflect better sensitivity. LG exhibited significantly impaired sensitivity to shape only in the manual estimation task. (B) The just noticeable difference (JND), reflecting resolution of hand aperture for object width, showed that LG has impaired resolution in the manual estimation task, but not in the grasping task. (C) LG performed normally in different aspects of the grasping task including reaction time (left), time taken to reach the maximum grip aperture (MGA, middle) and overall movement time (right), suggesting that his preserved sensitivity to the dimensions of objects cannot be accounted for by a speed-accuracy tradeoff.

perceptual abilities are profoundly impaired. Yet, it could be argued that LG's sensitivity to object shape in the grasping task was mediated by a speed-accuracy tradeoff. In particular, LG might gain his sensitivity to object shape by performing slower grasping movements, or delaying his MGA until the end of his movement. To rule out these alternative explanations we further analyzed the kinematic properties of the grasping movements. LG's reaction time, movement time, and the time taken to reach the MGA were found to be in the normal range and very close to the controls' mean in each of these parameters [all t 's < 1, Fig. 2C], suggesting that his preserved sensitivity could not be accounted for by such a speed-accuracy tradeoff.

3.4. Planning-control dissociation during grasping movement

In a series of theoretical and experimental studies, Dixon and Glover have argued that the planning of an action and the online control of the same action rely on two independent visual representations. According to this account, the early stages of the grasping movement can be influenced by perceptual factors which affect the planning stage, while the on-line control representation is not affected by these factors (e.g., Dixon & Glover, 2009; Glover, 2002, 2004; Glover & Dixon, 2001; Glover, Rosenbaum, Graham, & Dixon, 2004). According to this hypothesis, it could be argued that LG would exhibit reduced sensitivity to object shape at early stages of the grasping movement and preserved sensitivity later on during the movement. On the other hand, normal participants would gain sensitivity to object shape at earlier stages of the movement, presumably based on their intact perceptual processing of the Efron block shape. To test this prediction, we calculated the linear slope separately at different time points during the execution of the movement (see Methods for details). This analysis showed that the control participants began to show sensitivity to object shape (i.e., linear slopes larger than zero) at about 20% of the movement time. LG, however, was less sensitive to object shape compared to the controls in the first two thirds of the movement, showing a reduced linear slope compared to the controls. To statistically compare between LG's performance and that of the controls, we first averaged the slopes in each third of the movement (i.e., 10%–30%, 40%–60%, 70%–90%), and then applied the Crawford single-case test. To account for the problem of multiple comparisons we applied the Bonferroni correction. This analysis revealed that LG showed a reduced slope compared to the controls in the first [$t(8) = 3.795$, $p < .05$ (corrected)] and second parts of the movement [$t(8) = 3.08$, $p < .05$ (corrected)]. In contrast, LG showed intact linear slope, similar to that of the controls in the third part of the movement time [$t < 1$, $p > .4$ (corrected)] (see Fig. 3A, and Fig. 4A–C for the grasping aperture of the controls relative to LG).

Recently, Whitwell and Goodale (2013) have shown that the normalization of grasping movement time course could produce false sensitivity to object size at different phases of the movement trajectory. However, when movement normalization is conducted such that the MGA is taken as the end point of the movement (100%), this false sensitivity is eliminated. Hence, we reanalyzed our data using the MGA as the end

point, to ensure that the differences observed between LG and the controls were not induced by the normalization procedure. This analysis is presented in Fig. 3B and replicates LG's reduced slope in the first two thirds of the movement [$t(8)$'s > 3.13, p 's < .05 (corrected)], followed by a normal slope in the last third of the movement [$t(8) < 1$, $p > .9$ (corrected)].

These results suggest that LG's perceptual difficulties could interact with his grasping performance at the early stages of the movement trajectory, and therefore provide support for the planning-control dissociation proposed by Glover and Dixon (2001). We further elaborate on this issue in the Discussion section below.

4. Discussion

The present study aimed to test if vision-for-action, presumably mediated by the dorsal pathway, could develop normally even when vision-for-perception, presumably mediated by the ventral stream, does not. We examined the perceptual and the visuomotor sensitivity to the width of graspable objects in LG, a young man with a rare disorder of developmental object agnosia. Although LG was profoundly impaired in his perceptual sensitivity to the width of graspable objects, his visuomotor sensitivity was comparable to that of the controls. These results are in-line with previous investigations that show that at least some aspects of the segregation between vision-for-perception and vision-for-action emerge early in life (Hadad et al., 2012).

4.1. The planning-control dissociation

Previous studies that investigated goal directed actions in general, and grasping in particular, focused their analysis on the MGA, mainly because this point in the movement trajectory consistently reflects sensitivity to the relevant dimension of the target object (Jakobson & Goodale, 1991; Jeannerod, 1984, 1986) and is not confounded by other movement factors such as aperture velocity (Ganel et al., 2014). Yet, in the last decade more studies went beyond the MGA and systematically analyzed the hand aperture across the grasping movement, revealing interesting changes in the characteristics of the grasping movement during its execution (e.g., Dixon & Glover, 2009; Franz, Scharnowski, & Gegenfurtner, 2005). Dixon, Glover and colleagues (Dixon & Glover, 2009; Glover, 2002, 2004; Glover & Dixon, 2001; Glover et al., 2004), employed movement trajectory analysis and found a dissociation between planning and online control, leading them to suggest that these two stages rely on different visual representations.

In contrast to previous studies examining action-perception dissociations in visual agnostic patients by mainly focusing on the MGA (Goodale et al., 1991; Karnath et al., 2009; Lê et al., 2002), in the present study we went beyond the MGA to obtain a wider range of spatio-temporal observations along the movement trajectory. We found that LG's sensitivity to object shape during grasping was evident at a later stage of the movement execution time compared to that of the matched controls, and that his sensitivity to object shape was comparable to that of the controls only after 60% of the movement

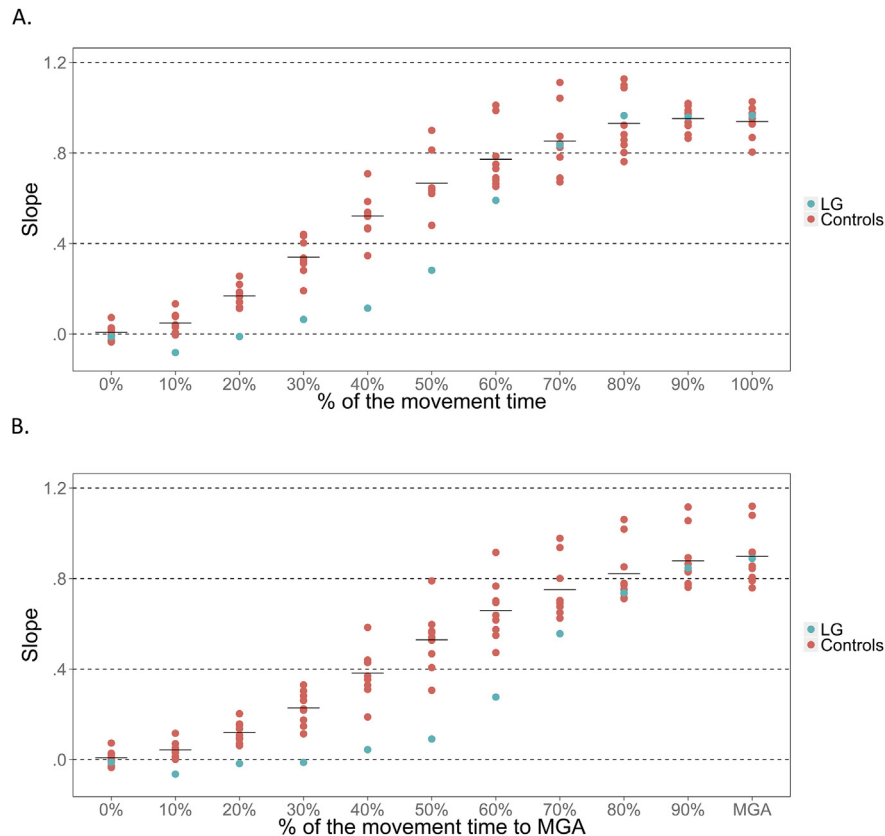


Fig. 3 – (A) Average slope of the grip aperture data along the movement trajectory. In controls ($n = 9$), grasping apertures began to be scaled to object width at about 20% of movement time (i.e., average slope is larger than zero), and reached a peak (MGA) at about 70% of the movement time. Although LG exhibited a significantly late sensitivity to object shape (his aperture was scaled to object width only at around 60% of the movement time), he reached the MGA at a time comparable to that of the controls. (B) Similar results were obtained when the normalization of the movement trajectory was based on the MGA as the final point of the movement. Notations as in Fig. 2.

had been completed. Importantly, this delayed sensitivity could not be attributed to a speed-accuracy trade-off since LG's reaction time, time taken to reach the MGA, and the total movement time were not different from those of the controls. Moreover, the fact that LG did not differ from the control participants in any of these aspects means that the differences that emerged between LG's aperture profile and those of the control participants could not have been an artifact of the normalization procedure (Whitwell & Goodale, 2013) and this was also confirmed in an additional analysis that set the MGA as the end point of the movement (see the Results section for details). All of these suggest that LG's failure to show sensitivity to the shape of the object early in the execution of the grasping movement can be explained by his compromised perceptual abilities, consistent with Dixon and Glover's conjecture that this part of the movement is influenced by perception of the shape and the size of the target object.

While a systematic analysis of the aperture profiles over different grasping tasks has not been reported in the well-studied case of patient DF, such an analysis was conducted in another patient (JS) with acquired visual form agnosia following bilateral lesion to the medial aspects of the ventral occipitotemporal cortex (Karnath et al., 2009). That study did not report the linear slope for each point in the aperture

profiles, but the overall reported trend seems to show a delay in the emergence of sensitivity to object shape as we have observed in LG.

Lastly, it is important to note that the planning-control model and the action-perception model can both account for the overall performance observed for LG. In particular, according to the perception-action model, LG is impaired in the perceptual task since this task relies on the ventral pathways' neural mechanisms, which function abnormally in LG. The perception-action model further posits that the normal aspects of his grasping movements predominantly rely on his dorsal pathway mechanisms. The planning-control model complements these arguments. It suggests that during manual estimation the on-line control mechanisms do not come into play since the movement is not directed towards an object, and this in turn means that there would be no online correction during this task. In the grasping, when the movement is directed towards a target object, the online control mechanisms play a role and become dominant during the movement.

Taken together, LG's behavior reflects two important dissociations. The first is a dissociation between object perception and visuomotor control. LG exhibits profoundly impaired shape perception alongside a preserved visuomotor sensitivity to object shape (Fig. 2). This dissociation is best accounted for

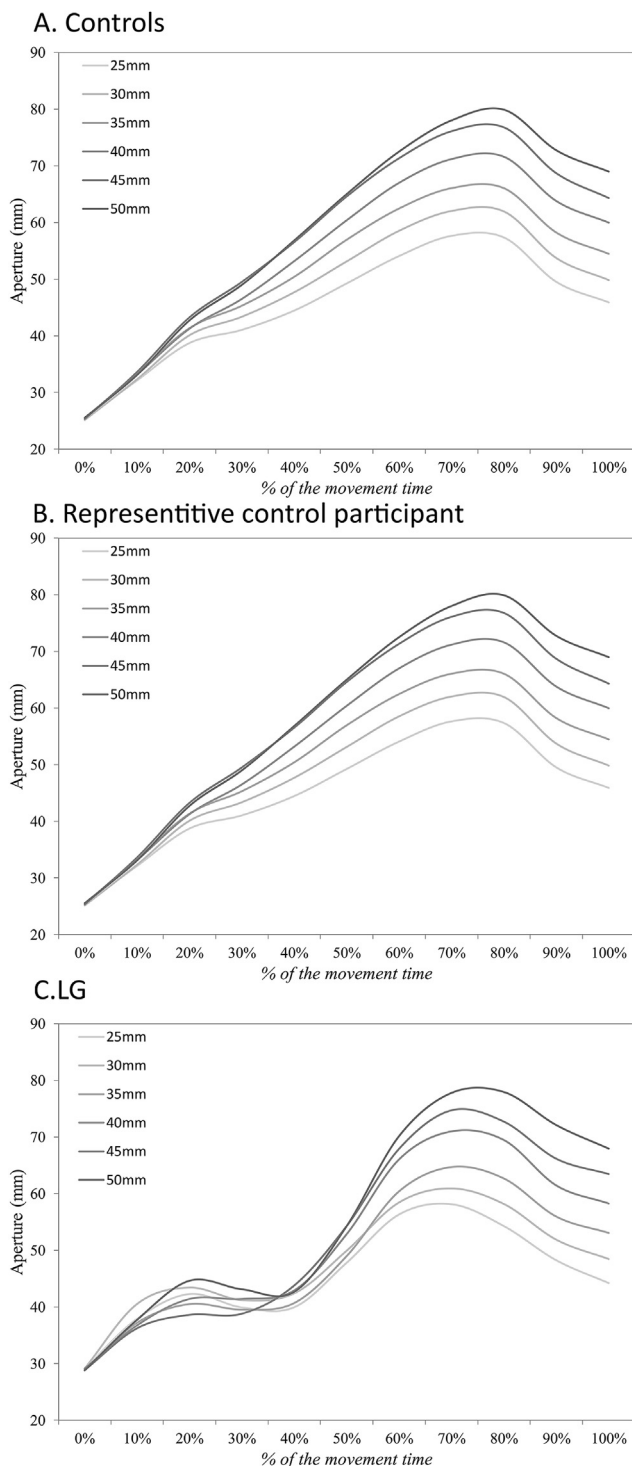


Fig. 4 – Grip apertures along the movement trajectory for each object size. (A) Grip aperture was averaged across all control participants. (B) Grip apertures of a representative control participant. (C) Grip apertures of LG. The graph demonstrates that LG's sensitivity to size is achieved relatively late along the movement trajectory, echoing the results of the slope analysis.

by the perception-action model. The second dissociation relates to LG's grasping behavior. In particular, LG's sensitivity to object shape evolved considerably late in the grasping movement compared to matched controls (Fig. 3). This finding strongly supports the planning-execution model and suggests that grasping on-line control mechanisms could be dissociated from the initial planning phase mechanisms, at least within the particular grasping task that we used.

4.2. JND as a tool for the investigation of size resolution in grasping and perceptual tasks

Previous studies that utilized the Efron task to investigate sensitivity to object width (and thus shape) in acquired visual object agnosia patients, measured sensitivity to shape by calculating the linear slope (as was done here) or the correlation between hand aperture and object width (Goodale et al., 1991; Karnath et al., 2009). In the present investigation, we further extended the analyses that measure the resolution of response in the estimation and grasping tasks by calculating the JNDs based on the within-subject standard deviations of the hand aperture. The use of JND as a tool to investigate the resolution of the scaling of hand aperture to object width was first proposed in the context of Weber's law (Ganel et al., 2008), and recently has also been used in other tasks (Freud & Ganel, 2015; Ganel & Goodale, 2014). In line with the linear slope analysis, the JND analysis showed that in LG the scaling of the hand aperture during grasping exhibited normal resolution to object shape, but profoundly impaired resolution in the manual estimation task. These results indicate that the JND, defined here as the within-subject standard deviation to object width, could be used as an additional measure of sensitivity to objects' dimensions, even in clinical populations.

4.3. The role of on-line visual feedback in the perception-action dissociation

There is an ongoing debate in the literature about the role of on-line visual feedback in the observed dissociation between vision-for-action and vision-for-perception. For example, Franz and colleagues demonstrate that grasping movements are affected by the Müller-Lyer illusion when visual feedback is denied and that the apparent insensitivity of grasping to this illusion that others have reported occurs only when on-line visual feedback is available, allowing participants to correct their movements (Franz, Hesse, & Kollath, 2009). Thus, according to their account, the delayed size sensitivity of the grip scaling in LG could be interpreted as evidence that this sensitivity relied only on the availability of visual feedback.

Evidence from previous investigations, however, and from the current study suggests that despite the importance of visual feedback to grasping, the functional dissociation between vision-for-action and vision-for-perception cannot be explained solely on this basis (Westwood & Goodale, 2011). In particular, it has been demonstrated in a number of studies that the action-perception dissociation can be observed even when vision is occluded at the time of movement initiation (i.e., open-loop grasping) (Chen, Sperandio, & Goodale, 2015; Ganel, Chajut, Tanzer, & Algom, 2008; Glover & Dixon, 2001; Hu, Eagleson, & Goodale, 1999). In fact, this is also true for DF

(Whitwell et al., 2015, but see Hesse et al., 2012; Schenk, 2012). Moreover, in the present study, LG's average time to reach the MGA was similar to that of the control participants, and so despite not receiving prolonged on-line visual information relative to the control participants, LG still exhibited intact sensitivity to object shape as reflected by the linear slope and the JND, while a different pattern was observed in the perceptual task, in which visual feedback was also available.

An additional reason that led us to utilize the close-loop design in the present study is that this setting can be considered as more ecological, and as it more closely reflects grasping performance in real-world situations, it provides better insights about real-world and everyday behavior and performance. Nevertheless, future studies should directly test this issue by examining LG's grasping performance in different tasks and under open-loop conditions.

4.4. The contribution of intermediate visual areas to higher level functions

The full field representations of retinotopic related areas as V1, V2, and V3 (lower half in the dorsal and upper half in the ventral aspect) are assumed to be contributing in a similar manner to dorsal and to ventral functions. Therefore, it may seem unclear how LG's intermediate visual areas (V2/V3) which function in a significantly abnormal manner (Gilaie-Dotan et al., 2009, 2013), seem to adversely affect only ventral-related functions while sparing dorsal-related functions. A few possibilities might give rise to this apparent ambiguity. One possibility is that dorsal related functions do not rely on intermediate retinotopic areas as much as ventral related functions do. This might either stem from non-sequential or non-hierarchical integration of information in the dorsal stream (Gilaie-Dotan, in press), or perhaps from magnocellular integration in the dorsal pathway that might be more reliant on global or coarse integration, while ventral related functions might be more sensitive to, and therefore reliant on fine integration (Previc, 1990). Such a scenario, where ventral functions are highly reliant on hierarchical fine spatial integration of information (Previc, 1990) and dorsal functions are not, could explain why ventral functions would be dependent on intermediate visual areas' functioning, and dorsal functions would not. In LG's case it is therefore expected that the abnormal functioning of his intermediate visual areas (Gilaie-Dotan et al., 2009, 2013) would adversely affect his ventral but not his dorsal related functions. Another possibility is that subcortical bypasses through the pulvinar (Van Essen, 2005) allow dorsal (but perhaps not ventral) high-order areas to function normally. Furthermore, it is also worth noting, that not all of LG's ventral functions are actually impaired, as for example his color perception seems to be spared (Gilaie-Dotan, in press), and on the other hand maybe not all his dorsal functions are normal – as there are ones that have not yet been tested.

5. Conclusions

The current investigation provides novel evidence that perception and action related to object shape are dissociable.

Such dissociation can develop even when vision-for-perception and the functions of the ventral pathway are severely compromised. Yet, the current results also point to a dissociation between different components of the grasping movements, further demonstrating the distinction between planning and online control. Taken together, these findings suggest that the observed functional and neuroanatomical dissociation between vision-for-action and vision-for-perception is likely to reflect a fundamental organizational principle of the visual system.

Acknowledgments

We would like to thank Melvyn A. Goodale for fruitful discussions and his comments on early drafts of this manuscript. We would also like to thank LG for his time and participation in this study.

REFERENCES

- Ariel, R., & Sadeh, M. (1996). Congenital visual agnosia and prosopagnosia in a child: a case report. *Cortex*, 32(2), 221–240.
- Aviezer, H., Hassin, R. R., & Bentin, S. (2012). Impaired integration of emotional faces and affective body context in a rare case of developmental visual agnosia. *Cortex*, 48(6), 689–700.
- Aviezer, H., Hassin, R. R., Perry, A., Dudarev, V., & Bentin, S. (2012). The right place at the right time: priming facial expressions with emotional face components in developmental visual agnosia. *Neuropsychologia*, 50(5), 949–957.
- Brooks, J. L., Gilaie-Dotan, S., Rees, G., Bentin, S., & Driver, J. (2012). Preserved local but disrupted contextual figure-ground influences in an individual with abnormal function of intermediate visual areas. *Neuropsychologia*, 50(7), 1393–1407.
- Chen, J., Sperandio, I., & Goodale, M. A. (2015). Differences in the effects of crowding on size perception and grip scaling in densely cluttered 3-d scenes. *Psychological Science*, 26(1), 58–69.
- Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, 40(8), 1196–1208.
- Crawford, J. R., & Garthwaite, P. H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: evaluation of alternatives using Monte-Carlo simulations and revised tests for dissociations. *Neuropsychology*, 19(3), 318–331.
- Culham, J. C., Danckert, S. L., De Souza, J. F., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153(2), 180–189.
- Dijkerman, H. C., Lê, S., Démonet, J. F., & Milner, A. D. (2004). Visuomotor performance in a patient with visual agnosia due to an early lesion. *Cognitive Brain Research*, 20(1), 12–25.
- Dixon, P., & Glover, S. (2009). Perseveration and contrast effects in grasping. *Neuropsychologia*, 47(6), 1578–1584.
- Efron, R. (1969). What is perception?. In *Proceedings of the Boston Colloquium for the Philosophy of Science 1966/1968* (pp. 137–173). Springer.

- Farah, M. J. (1994). *Visual agnosia* (2nd ed.). Cambridge, MA: MIT Press/Bradford Books.
- Franz, V. H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control. *Neuropsychologia*, 47(6), 1518–1531.
- Franz, V. H., Scharnowski, F., & Gegenfurtner, K. R. (2005). Illusion effects on grasping are temporally constant not dynamic. *Journal of Experimental Psychology: Human Perception and Performance*, 31(6), 1359.
- Freud, E., & Ganel, T. (2015). Visual control of action directed toward two-dimensional objects relies on holistic processing of object shape. *Psychonomic Bulletin & Review*, 1–6.
- Freud E., Ganel T., Shelef I., Hammer M.D., Avidan G., Behrmann M., Three-Dimensional representations of objects in dorsal cortex are dissociable from those in ventral cortex, *Cerebral Cortex* 2015. in press.
- Gallivan, J. P., & Culham, J. C. (2015). Neural coding within human brain areas involved in actions. *Current Opinion in Neurobiology*, 33, 141–149.
- Ganel, T., Chajut, E., & Algom, D. (2008). Visual coding for action violates fundamental psychophysical principles. *Current Biology*, 18, R599–R601.
- Ganel, T., Chajut, E., Tanzer, M., & Algom, D. (2008). Response: when does grasping escape Weber's law? *Current Biology*, 18(23), R1090–R1091.
- Ganel, T., Freud, E., Chajut, E., & Algom, D. (2012). Accurate visuomotor control below the perceptual threshold of size discrimination. *PLoS One*, 7(4), e36253.
- Ganel, T., Freud, E., & Meiran, N. (2014). Action is immune to the effects of Weber's law throughout the entire grasping trajectory. *Journal of Vision*, 14(7), 11.
- Ganel, T., & Goodale, M. A. (2003). Visual control of action but not perception requires analytical processing of object shape. *Nature*, 426, 664–667. <http://dx.doi.org/10.1038/nature02156>. nature02156 [pii].
- Ganel, T., & Goodale, M. A. (2014). Variability-based Garner interference for perceptual estimations but not for grasping. *Experimental Brain Research*, 232(6), 1751–1758.
- Gilaie-Dotan S., Which visual functions depend on intermediate visual regions? Insights from a case of developmental visual form agnosia, *Neuropsychologia* 2015 (in press).
- Gilaie-Dotan, S., Bentin, S., Harel, M., Rees, G., & Saygin, A. P. (2011). Normal form from biological motion despite impaired ventral stream function. *Neuropsychologia*, 49(5), 1033–1043.
- Gilaie-Dotan, S., Hahamy-Dubossarsky, A., Nir, Y., Berkovich-Ohana, A., Bentin, S., & Malach, R. (2013). Resting state functional connectivity reflects abnormal task-activated patterns in developmental object agnosia. *NeuroImage*, 70, 189–198.
- Gilaie-Dotan, S., Perry, A., Bonne, Y., Malach, R., & Bentin, S. (2009). Seeing with profoundly deactivated mid-level visual areas: non-hierarchical functioning in the human visual cortex. *Cerebral Cortex*, 19, 1687–1703.
- Glover, S. (2002). Visual illusions affect planning but not control. *Trends in Cognitive Sciences*, 6(7), 288–292.
- Glover, S. (2004). Planning and control in action. *Behavioral and Brain Sciences*, 27(01), 57–69.
- Glover, S. R., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. *Journal of Experimental Psychology: Human Perception and Performance*, 27(3), 560–572. <http://dx.doi.org/10.1037/0096-1523.27.3.560>.
- Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research*, 154(1), 103–108.
- Goodale, M. A. (2014). How (and why) the visual control of action differs from visual perception. *Proceedings of the Royal Society B: Biological Sciences*, 281(1785), 20140337.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 20–25.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349(6305), 154–156.
- Hadad, B.-S., Avidan, G., & Ganel, T. (2012). Functional dissociation between perception and action is evident early in life. *Developmental Science*, 15(5), 653–658.
- Hanisch, C., Konczak, J., & Dohle, C. (2001). The effect of the Ebbinghaus illusion on grasping behaviour of children. *Experimental Brain Research*, 137(2), 237–245.
- Hesse, C., Ball, K., & Schenk, T. (2012). Visuomotor performance based on peripheral vision is impaired in the visual form agnostic patient DF. *Neuropsychologia*, 50(1), 90–97.
- Himmelbach, M., & Karnath, H. O. (2005). Dorsal and ventral stream interaction: contributions from optic ataxia. *Journal of Cognitive Neuroscience*, 17(4), 632–640.
- Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research*, 126(1), 109–116.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Experimental Brain Research*, 86(1), 199–208.
- James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain*, 126(11), 2463–2475.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16(3), 235–254.
- Jeannerod, M. (1986). The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behavioural Brain Research*, 19(2), 99–116.
- Karnath, H.-O., Rüter, J., Mandler, A., & Himmelbach, M. (2009). The anatomy of object Recognition—Visual form agnosia caused by medial occipitotemporal stroke. *The Journal of Neuroscience*, 29(18), 5854–5862.
- Konen, C. S., Behrmann, M., Nishimura, M., & Kastner, S. (2011). The functional neuroanatomy of object agnosia: a case study. *Neuron*, 71(1), 49–60.
- Lê, S., Cardebat, D., Boulanouar, K., Hénaff, M.-A., Michel, F., Milner, D., et al. (2002). Seeing, since childhood, without ventral stream: a behavioural study. *Brain*, 125(1), 58–74.
- Lev, M., Gilaie-Dotan, S., Gotthilf-Nezri, D., Yehezkel, O., Brooks, J. L., Perry, A., et al. (2015). Training-induced recovery of low-level vision followed by mid-level perceptual improvements in developmental object and face agnosia. *Developmental Science*, 18(1), 50–64.
- Marks, L. E., & Algom, D. (1998). Psychophysical scaling. In M. H. Birnbaum (Ed.), *Measurement, judgment and decision making* (pp. 81–178). San Diego, CA: Academic Press.
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, 9(5), 555–604.
- van Polanen, V., & Davare, M. (2015). Interactions between dorsal and ventral streams for controlling skilled grasp. *Neuropsychologia*, 79, 186–191.
- Previc, F. H. (1990). Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. *Behavioral Brain Sciences*, 13, 519–541.
- Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Experimental Brain Research*, 174(1), 176–188.

- Schenk, T. (2012). No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *The Journal of Neuroscience*, 32(6), 2013–2017.
- Schenk, T., & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1(1), 52–62.
- Schum, N., Franz, V. H., Jovanovic, B., & Schwarzer, G. (2012). Object processing in visual perception and action in children and adults. *Journal of Experimental Child Psychology*, 112(2), 161–177.
- Smeets, J. B., & Brenner, E. (2008). Grasping Weber's law. *Current Biology*, 18(23), R1089–R1090.
- Stevens, S. S. (1975). *Psychophysics*. New York: Wiley.
- Striem-Amit, E., Dakwar, O., Reich, L., & Amedi, A. (2012). The large-scale organization of “Visual” streams emerges without visual experience. *Cerebral Cortex*, 22(7), 1698–1709.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Utz, K. S., Hesse, C., Aschenneller, N., & Schenk, T. (2015). Biomechanical factors may explain why grasping violates Weber's law. *Vision Research*, 111, 22–30.
- Van Essen, D. C. (2005). Corticocortical and thalamocortical information flow in the primate visual system. *Progress in Brain Research*, 149, 173–185.
- Westwood, D. A., & Goodale, M. A. (2011). Converging evidence for diverging pathways: neuropsychology and psychophysics tell the same story. *Vision Research*, 51(8), 804–811.
- Whitwell, R. L., & Goodale, M. A. (2013). Grasping without vision: time normalizing grip aperture profiles yields spurious grip scaling to target size. *Neuropsychologia*, 51(10), 1878–1887.
- Whitwell, R. L., Milner, A. D., Cavina-Pratesi, C., Barat, M., & Goodale, M. A. (2015). Patient DF's visual brain in action: visual feedforward control in visual form agnosia. *Vision Research*, 110(Part B), 265–276.
- Yeatman, J. D., Weiner, K. S., Pestilli, F., Rokem, A., Mezer, A., & Wandell, B. A. (2014). The vertical occipital fasciculus: a century of controversy resolved by in vivo measurements. *Proceedings of the National Academy of Sciences of the United States of America*, 111, E5214–E5223.