HOW VISUAL INFORMATION IS TRANSFORMED INTO MOTOR ACTS

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ABSTRACT

Behavioural and neuroscience research just starts to unravel the intriguing nature of how visual information is processed into motor acts. The two visual system hypothesis suggests the processing of visual information into two distinct streams in the human brain. One dorsal stream dealing with online control of motor control and a ventral stream responsible for perception. However recent research shows increasing evidence for a needed interaction between the two streams. Anatomical studies give evidence of a significant connection between the two streams. Second, research of immediate and delayed grasping behaviour with fMRI measurements revealed communication between regions of the dorsal and ventral stream. Especially for (complex) controlled grasping behaviour, tool use and recognition interaction is needed to complete the processing of spatial information for visual motor control. This behaviour is not possible without involvement of structures of the ventral stream. The connections between the dorsal stream to and from lateral occipital complex (LOC) area of the ventral stream are an important region of focus and future research will give us new insights on this complex issue.

Keywords: **Visual processing, dorsal stream, ventral stream, dorsal ventral interaction, LOC, grasping behaviour**

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Introduction

The amazing nature of processing visual information is still dazzling our brain. Millions of cells are working together in a well-organized way to give us a perception of the world around us. Even more interesting is how this visual information is used to control motor movement of our body and second what our perception is of these processes. One may think that at a certain moment a stimuli enters the brain and creates an image of the world around us. This image then serves as a conscious representation of what we see and is used to decide which action has to be taken. This leads to control of the motor output and initiates the action necessary at that specific moment. However Ungerleider and Mishkin et al. and Goodale et al. argued that this view of how visual information is transformed into motor acts is not correct. There is quite a distinction between the visual pathways used to perceive the world and those controlling motor action (Goodale, 2008). The latter set an important theory in 1992 which stated a two vision system separated by a dorsal and ventral stream for action and perception. The information used to control movements is processed in a different way than the information which is used to percept objects (Polanen, 2015). This theory will have further implications about our percept of the world. Is the motor action performed the same as we perceive? And how is visual information transformed into motor acts? Is it even possible that our brain processes visual information into motor movement without even reaching the conscious perception?

Accurate grasping behaviour makes us possible to operate in an always moving world. At the same time humans are efficient in recognize objects and building a perception of the world. But after all it is the immediate action which matters and not the thought about it (Goodale, 2008). Because in normal life our movement and behaviour is the outcome of these actions. Patients with damage to brain areas involved in these processes can struggle even with simple hand movements and or reaching and grasping of objects and tools. Or in contrast having problems with recognizing objects and faces.

To investigate this only by psychophysical research is not enough. This provides us with information obtained on conscious report. We need neuro-imaging experiments to give us any insight into the visual control of movement, the pathways involved and how and where these are located in our brain. The use of the fMRI gives us a much more complete image of which visual regions are involved. This combined with neuropsychology and neurophysiology experiments on humans and monkeys will offer more insight into this subject.

However the strict discrepancy between the two visual pathways may also be a simplification of the reality, because the separation of the two pathway´s is not totally and some functions are ascribed to both pathways. Even some structures are not exclusive to one of the two pathways. The degree to which the both streams are connected or separated is still a point of debate. Some neurons are even projecting to cells of layers in both pathways proposed to be separated. Takemura and coworkers have shown that a major white matter pathway connects the dorsal and ventral visual cortex, coding information of object properties and spatial information(Takemura, 2015). Cloutman et al. also argue pro some degree of interaction between the both streams(Cloutman, 2013; Takemura, 2015). This makes the 25 years old model of the two vision system still point of debate.

This essay will give an overview of the latest research on how visual information is transformed into motor acts and if or where the dorsal and ventral streams interact from a neuroscientific and biological perspective.

From the eye to the visual cortex

To explore this subject, first start with explaining how a visual stimuli exactly reaches our visual cortex and creates an image of the world. The detailed image we received when we look around us starts with collecting light by the retina of the eyes. The visual perception begins with sensitivity to a stimulus of neurons in the retina. The retina consist of two types of photoreceptors, rods and cones, which are structural different and therefore correlate with important functional differences. Cones are sensitive for different wavelengths of light and are responsible for seeing color. Rods are more sensitive for light thus need less light. After hyperpolarization of one of 125 million photoreceptors the signal is funneled to 1 million ganglion cells of 3 types, Magnocellular, Parvocellular and nonM-nonP ganglion cells. P and nonM-nonP cells have a small receptive field and are mainly involved in information about color and shape and M cells have a large receptive field and carry information about movement. The signal is parallelly processed towards the visual cortex via the so called retinofugal projection. This important feature of the brain determine the way we perceive the world around us because the visual input is parallelly processed from retina to striate cortex V1. As we will see later on this also determine the way we control and perceive motor action acts. For example P cells are suited for discrimination of fine detail and M cells can detect small changes in contrast over their large receptive field, contribute to low resolution vision.

The signal of the ganglion cells is continuing through the optic nerve and information from both eyes is combined at the optic chiasm. The information from the left visual hemifield is directed to left hemisphere and from the right into the right hemisphere, via the optic tract which innervate the lateral geniculate nucleus (LGN) of the dorsal thalamus. Information reach the LGN and after processing the visual information, projects it via axons to the primary visual cortex also called V1 located in Bradman's area 17. When we take a closer look we see a functional separation in de LGN which reveals parvocellular layers, magnocellular layers and koniocellular layers. It appears that the M ganglion cells in the retina projects exclusively to M layers of the LGN and P ganglion cells to P layers and nonM-nonP project to koniocellular layers. The pathway originating from the M type ganglion cells is called the magnocellular pathway and is in most part responsible for motion. The one originating from nonM-nonP is called the Blob pathway and is partially responsible for color. And last the pathway from P type cells is called the Parvo pathway and is responsible for shape. These separate pathways showed that the signals from different receptors of the eye are still parallely processed (Neuroscience, 2001; (Merigan, 1993). This separation is continued in the visual cortex in a couple of systems called the ventral "what" pathway receiving information of the parvo and blob pathway and the dorsal "where" pathway receiving information of the magnocellular pathway as stated by Ungerleider and Mishkin as the two vision system. The ventral stream is processing information about an objects features (what), like shape texture and color and contains structures in the V4 area. The dorsal stream is processing information about the spatial location of object (where) and their location respectively to the observer and contains structures in the visual V3 area and posterior intraparietal sulcus (pIPS) (Goodale, 2011). A great difference between the two streams processing visual information is the use of different type of ganglion cells. And it appears that the pathway from light hitting the eye to processing visual information in the visual cortex is almost entirely separated.

Visual perception and visual control

Goodale and Milner took the theory to the next level by proposing that the ventral "what" stream is responsible for visual perception and the visual control of action depends on the dorsal "where" stream. Hereby separating the visual pathway´s in the cerebral cortex and rewriting the model to the target where perception is applied. This proposal confirms the different roles of the ventral and dorsal streams and differentiates the function of visual perception and visual control in a behavioural context (Goodale, 1992; Goodale, 2004b; Goodale, 2008).

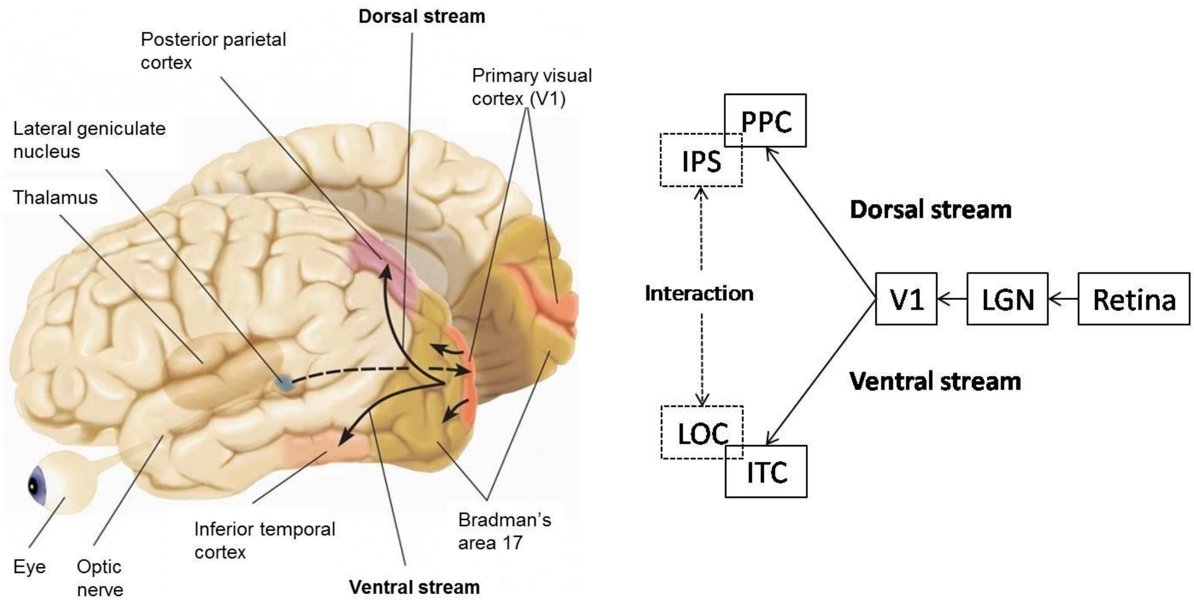

Fig 1. On the left the locations of the of the dorsal and ventral stream in the human brain on a 3D model of the brain. Light hitting the retina sends signal via the thalamus to the LGN which project to the primary visual cortex. Within the cerebral cortex the ventral stream arises from early visual areas V1 and projects to inferior temporal cortex. The dorsal stream also arises from early visual areas V1 but projects instead to the posterior parietal cortex. On the right a schematic representation of the proposed interaction between de 2 streams. Interaction can take place via the vertical occipital fasciculus (VOF) between the intraparietal sulcus (IPS) region of the dorsal stream and the lateral occipital complex (LOC) region of the ventral stream. The routes indicated by the arrows involve a series of complex interconnections. IPS, intra parietal sulcus; LOC, lateral occipital complex; PPC, posterior parietal cortex; ITC, inferior temporal cortex; LGN, Lateral geniculate nucleus. (adapted from Goodale, 2004a)

Vision for perception (ventral)

The ventral stream is involved in the perception of the visual world and the awareness and recognition of objects. The function of the ventral stream is to categorize objects in a scene based reference and together with higher order motor areas to construct the rich and detailed representations of the world that allow us to identify objects (Goodale, 2011) The ventral stream can be seen as an extension of combining features of the parvo pathway and blob pathway interpreting the properties of color and form of objects. The system computes the size, location and shape and orientation of objects in a scene based way. Perception does not take into account the size and place of an object in relation to its location but compares it which other objects, parts, and surfaces in the scene (Ganel, 2003). The vision for perception system is essential for accumulation a visual knowledge about our environment and has a behavioural utility in the role for planning and decision making. It is this stream which makes us conscious of the world around us and our actions. However perception does not require direct action, it may be necessary to recognize objects on a longer time scale then needed for online control of action (Goodale, 2008). So the time period over which a percept is constructed can be much longer in some cases. Thus by operating in an “offline”mode, using memory and a scene based location of objects, the ventral stream plays an important role in constructing our visual percepts.

Vision for action (dorsal)

Instead, the dorsal stream plays a critical role in the real time control of action. Because one can image that vision for action has to operate in an active direct “online” state to generate skilled actions. The dorsal stream gives direct information about the coordinates of the object which can often change fast from moment to moment. For this reason it is necessary that the required coordinates for the action are used immediately before the movement is initiated (Goodale, 2008). If we go back to the pathway from eye via LGN to V1 we can say that the function of the magnocellular pathway based on the capacities of the neurons involved is the control of motion. The dorsal stream can be seen as an extension of this pathway, e.g. having transient response, relatively large receptive fields, and a high percentage of direction selective neurons. The analysis of objects motion, the guidance of motor action and the spatial attention is ascribed to this pathway (neuroscience, 2001;(Takemura, 2015). Thus the dorsal pathway, which involves structures of the motor control, creates direct online action, hereby mediating the visual control of actions such as grasping of objects. To grasp an object with success it is essential that the system knows in an “online” mode about the spatial properties of an object such as the metrics and the frame of reference in relation to the observer, also called an egocentric view. The egocentric coordinates of an object can change fast from moment to moment. Of second importance is that the system operates on a fast time period and responds to changes in locations of an object but not to its color for instance. Studies with the macaque already make a suggestion that the dorsal stream receives the information about color information from areas in the ventral stream (Toth, 2002). Taken together this makes the visual motor system of the dorsal stream responsible for skilled and rapid actions.

Prove for theory: Patients and behavioural studies

Important key piece information for the understanding of how vision for action and perception works comes from research on patients with lesions in the dorsal or ventral stream. For example patients with neglect can suffer from optic ataxia which is caused by damage to the dorsal stream, leaving the ventral stream intact. These patients have still intact objects recognition, but have problems with grasping the object. Observations of these optic ataxia patients, I.G. and F.S, show that these patients improve in tasks when they are asked to execute an action towards memorized stimuli (Rossit, 2011). This is in contrast with a patient, D.F., with visual agnosia and bilateral lesions within lateral occipital complex (LOC) which is part of the ventral stream. DF is not able to recall from memory but nevertheless is able to grasp object in real time control (Goodale, 2004b). This gave evidence to the 2 model system in which real time actions rely on processing carried out in the dorsal visual stream and memory guided actions make use of the ventral stream, involved in the perceptual representation and object perception.

BOX 1: Patients

A great contribution to research of the ventral and dorsal stream comes from patients with lesions affecting one or the other of the two streams. Patient D.F. with damage to the ventral stream including the LOC area developed a profound form of visual agnosia. Even though functions of contrast sensitivity and low visual abilities are still intact, she has problems with object recognition. For example when asked to indicate how to put a card into a slot or indicate the appropriate grip seizure to grasp a cup, patient D.F. could not indicate the right orientation of the card or the grip seizure of her hand. Nonetheless she could move her hand and or the card appropriately to interact when immediate interaction is required and her action is almost indistinguishable from normal controls. This is suggesting that the regions which are damaged in D.F. brain normally contribute to a system which is involved in perception. In contrast patient F.S and I.G with damage to the dorsal stream suffer from optic ataxia, a deficit in visually guided hand movements. For example they miss target objects by inches when reaching immediate and show poor grip and hand orientation when attempting to grasp objects. Remarkable, they can even act better then healthy persons when the patients were asked to perform an action towards a memorized stimuli. These observations support that immediate action rely on processing carried out in the dorsal stream (Goodale, 2008; Rossit, 2011; Whitwell, 2014).

Second a number of investigators have used behavioural studies with a variety of tasks and responses to show the separation between perception of visual stimuli and the online action control following the stimuli (Goodale, 2004b). A famous example is an adjustment to the Ebbinghaus illusion studied by Aglioti, Desouza and Goodale (Aglioti, 1995). This is an optical illusion of relative size perception. The adjustments involved a graspable version of the illusion containing two circles of identical sized placed near each other. The left one is surrounded by larger circles while the right one is surrounded by smaller circles. As a result the central circle with large circles around appears smaller and the circle with larger circles appears bigger. The researches randomly changed the relative size of the central circle, so that in some trials the real size of the circles appeared perceptually identical in size, where as in some trials the real size appeared perceptually different in size. The results where astonishing, when asked to estimate the size with their thumb and index finger they were susceptible to the illusion, and thus perceived size distortion. However when subjects were asked to grasp the central circle something (amazing) appears, the distance between thumb and index finger, the maximum grip aperture, seems not affected by the illusion. This means that the Ebbinghaus illusion doesn't distort the real time action. The same results accounts for several other illusions, including the Ponzo illusion and the hollow face illusion. These studies provide support for the 2 vision system that supposed a separate dorsal stream for control of action and a separate ventral stream for conscious perception.

Delayed and immediate actions (hints for interactions)

Furthermore, this research shows that real-time online action control depends on pathways from the early visual areas through to relatively encapsulated visuo-motor mechanisms in the dorsal stream. These pathway's from eye to visual cortex, containing also motor centers in the premotor cortex and brain stem, are responsible for processing an objects metrics and spatial matter in the egocentric coordinates relative to the observer which have to perform the action. This real time control of immediate action is essential to operate accurate in a world where the location of an object often changes quickly and often with respect to the observer. On the other hand the delayed action relies much more on information stored in memory and make use of a perceptual representation of the object generated by the ventral stream. Unlike the online control mechanisms in the dorsal stream, perception based movements make use of relational metrics and scene based coordinates. This suggests that the ventral stream can plan and execute action upon an object when a delayed response is asked. However the pathways for the motor control are still part of the dorsal steam. This raises the question if in some situations the information from the ventral stream is needed in the dorsal stream. For instance when an object has to be grasped with a long delay (Rossit, 2011). Is the difference between delayed and immediate actions as straight and simple as stated above? Goodale etc. proposed that "the production of real time action to visible targets depends on pathways that are separate from those mediating memory driven action" this is also confirmed by Singhal with fMRI grasping experiments (Goodale, 2004b; Singhal, 2013). Thus according to the 2 vision model the ventral stream controls delayed action and the dorsal stream immediate action. However more complex and delayed grasping and tool use tasks need scene based information which is stored in the LOC of the ventral stream. Delayed actions are more influenced by relational metrics and scene based coordinates processed in the ventral stream (Singhal, 2013). Even more precise: To perform a delayed or tool use action the dorsal stream needs to initiate action information which is stored in the LOC of the ventral stream. Necessary for delayed actions are conceptual knowledge of the objects such as the relational metrics and scene based coordinates and this relies on interaction between ventral and dorsal areas. These studies all indicate that in grasping behaviour the dorsal and ventral stream seems to be mutually interacting. As behaviour becomes more complex and or tools are involved the ventral streams seems to be more involved because scene based and stored memory is needed to guide the grasping behaviour movement.

The research of Rossit et al with Patient F.S. add to this knowledge by stating that both grasping and reaching towards a target seems to be affected by optic ataxia in delayed actions but not in immediate actions (Rossit, 2011). This raises the question which regions in the ventral stream are important for (complex) delayed action. A region of interest is the previous mentioned LOC region. Second, unlike healthy controls, neclet patients D.F. and F.S. both showed impairment in delayed grasping experiments, which are facilitated by the ventral stream, suggesting damage to regions which make connection between the dorsal and ventral stream. This suggests that there needs to be some communication between the streams at the moment of time of action. In this patient the lesions take out anatomically some of the interaction between the dorsal and ventral stream and thus prove that there is interaction during time of action, because the motor control is believed to be primarily controlled by dorsal stream.

To emphasize that the field of research is still moving Almeida et al. plead for separate pathways based on the findings that magnular cells provide the dorsal stream of information. These cells operate with a low frequency, so in a grasping or tool task fMRI experiment, low frequency indicates input from the dorsal stream. However in 2013 they suggest that structures in the dorsal stream which compute motor relevant actions also influence processing of identification of objects which is managed by the ventral stream. Apparently we do not know exactly if for more complex and or delayed behaviour interaction has to take or takes place between the two streams (Almeida, 2010; Mahon, 2013a).

So do we have a case for interaction between the two streams? While we can assume from several experiments that there must be some interaction, where and how they interact both anatomically and functionally is still point of debate. As mentioned above the vision model of Goodale doesn't address the part where interaction between the two streams could be necessary for a certain more complex behavioural response. To get a better understanding if interaction between the dorsal and ventral stream is required for certain actions we will focus on where (anatomically) interaction can and or will take place.

Where (anatomical)
Several studies in the past have described white matter connectivity between dorsal and ventral regions, suggesting combining of information of objects recognition and spatial properties in macaque (Zhong, 2003). Some studies even suggest an interaction between dorsal and ventral at the end stage of perception. They suggest that signals from the ventral stream are sent to the AIP in the macaque brain which is homolog to the anterior IPS in human (Verhoef, 2011). A candidate region for receiving and sending information from the ventral located LOC area is the anterior IPS involved in sensorimotor control tasks. Direct connections between these areas are known from macaque brains, where the infero temporal and AIP are connected, and these are the homologues of the LOC and anterior IPS in humans (Borra, 2008). Even with the analogies between the macaque and human we want these regions identified in addition for the human brain. Recently published anatomical studies now report more specifically that the vertical occipital fasciculus (VOF) connecting the dorsal and ventral streams processing information of the ventral stream including form identity and color information, suggesting a major white matter pathway between the dorsal and ventral stream (Martino, 2013; Takemura, 2015). Using a special fMRI technique called fiber tractography it was possible to show that the connections seemed to be dense in the V3 area (Takemura, 2015). In addition objects recognition fMRI experiments show activation of both ventral LOC and dorsal V3 area. During a delayed action grasping and reaching experiment with healthy participants, brain regions of the human dorsal stream remain still involved in action even during delay. Indicating that immediate actions rely on the dorsal stream and delayed actions rely on the ventral and dorsal stream (Singhal, 2013). This data is consistent with studies with non-human primates. More proof about the need for anatomical connection between the two streams comes from a study of Saber which showed that saccade planning, which is believed to be processed by the dorsal stream V3 and anterior IPS, also activates regions in the ventral stream V4 region (Saber, 2015). Roth et al. used an fMRI experiment where the tested stimulus activation by tools and images of grasping tools, to see in which regions this object recognition information is processed. The study show that potential information of position and identity of tools can be found both in de ventral LOC and the dorsal anterior IPS, hereby confirm the anatomical connection noted by Takemura (Roth, 2015). Gallivan and coworkers studied the hypothesis that areas in the ventral LOC region represent object weight when this weight information only can be derived from touching the object processed by the dorsal stream. They found that mechanical properties of an object believed to be processed only in the dorsal stream is represented in the LOC area of the ventral stream even when no visual differences

where visual between the objects. This means two things, there is communication from dorsal stream structures to the LOC region and the ventral stream is associated with perception and object recognition is involved in this process (Gallivan, 2014). Another study investigates the connections between the dorsal and ventral stream by making use of the transcranial magnetic stimulation (TMS) and electroencephalograpic activity (EEG). The authors have found a connection between parietal cortex suited in the dorsal stream and the ipsi-lateral temporo-occipital cortex in the ventral stream and also suggesting communication of information between the dorsal and ventral streams. This is needed to successfully complete the processing of spatial information needed for visual motor control (Zanon, 2010).

Although Goodale proposed that the two streams have a great division of functional preferences, these anatomical and functional studies show a significant communication between the two streams. All of the above studies discussed give strong evidence for a needed connection between the streams to exchange information in reaching and grasping behaviour (Begliomini, 2014; Verhagen, 2013)

Conclusion

All of above studies suggest an anatomical basis for communication between the two streams. However Goodale et al. still hold a strong argument when they argue that a visual stimulus is straightly directed via the anatomical direct structures from eye to visual cortex, especially because this is functional for rapid and action specific behaviour (Whitwell, 2014). One of the original phenomena that motivated the proposal of a separation between ventral and dorsal visual streams was the dissociation between object prehension and object recognition (optic ataxia vs. visual form agnosia (Mahon, 2013b). There are new recent anatomical studies suggesting or even reporting connections between the dorsal and ventral stream. (Takemura, 2015)

Some of these interesting things, noted here may be looking contradictory. The original theory of Goodale still holds for interpreting a lot of the results of functional imaging, neurophysiology and neuroanatomy. Especially when rapid responses to grasp a visible target are necessary. However these studies examining mostly grasping and reaching directly to objects. Latest research with more complex behaviour indicate that the dorsal stream can't operate on his own and need stored information of the ventral stream. Complex tool using and grasping behaviour is not possible without involvement of structures as the LOC of the ventral stream. The broad range of information used in the dorsal and ventral streams may even overlap, because they both are useful for online control of action and identification of objects. With so much variability's and the complexity of vision and behaviour there is comprehensive space for theories of integration between the two streams.

The crux lies more in the design and interpretation of the experiments. Rapid online action for grasping for example does not need per se input from the ventral stream, however delayed grasping or more complex movement with tools e.g. require some information stored in the ventral stream. This is in line with the review of Polanen et al. where they stated that even more complex learned grasping behaviour still needs information which is stored in the ventral stream(Polanen, 2015).

An ongoing challenge of research is to show with fMRI techniques which brain areas resonance with the behavioural findings and merge this with knowledge already known from anatomical and neurophysiology studies of the dorsal and ventral stream. More insight in the anatomical question have to come from experiments which focus on where communication from or to the LOC area take place. Experiments, which address e.g. grasping, tool use and identity and weight lifting, can give us more definite answers.

All of these studies in human brains contribute to a better understanding of how information can be communicated between the dorsal and ventral stream and provide some initial starting points of where to look for interaction between brain regions. But we need further studies to give more insight in where and how this communication takes place resulting in knowledge that can contribute to health and disease.

REFERENCES

Aglioti, S. (1995). Size-contrast illusions deceive the eye but not the hand.(curr. bio.)

Almeida, J. (2010). The role of the dorsal visual processing stream in tool identification. *Psychological Science, 21*(6), 772-8.

Begliomini, C. (2014). An investigation of the neural circuits underlying reaching and reach-to-grasp movements: from planning to execution. *Frontiers in Human Neuroscience, 8*

Borra, E. (2008). Cortical connections of the macaque anterior intraparietal (AIP) area. *Cerebral Cortex, 18*(5), 1094-111.

Cloutman, L. L. (2013). Interaction between dorsal and ventral processing streams: where, when and how? *Brain and Language, 127*(2), 251-63.

Gallivan, J. P. (2014). Representation of object weight in human ventral visual cortex. *Current Biology, 24*(16), 1866-73.

Ganel, T. (2003). Visual control of action but not perception requires analytical processing of object shape. *Nature, 426*(6967), 664-7.

Goodale, M. A. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20-5.

Goodale, M. A. (2004a). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology, 14*(2), 203-11.

Goodale, M. A. (2004b). Two distinct modes of control for object-directed action. *Progress in Brain Research, 144*, 131-44.

Goodale, M. A. (2008). Action without perception in human vision. *Cognitive Neuropsychology, 25*(7-8), 891-919.

Goodale, M. A. (2011). Transforming vision into action. *Vision Research, 51*(13), 1567-87.

Mahon, B. Z. (2013a). Spatial frequency tuning reveals interactions between the dorsal and ventral visual systems. *Cognitive Neuroscience, Journal Of, 25*(6), 862-71.

Mahon, B. Z. (2013b). Spatial frequency tuning reveals interactions between the dorsal and ventral visual systems. *Cognitive Neuroscience, Journal Of, 25*(6), 862-71.

Martino, J. (2013). Wernicke perpendicular fasciculus and vertical portion of the superior longitudinal fasciculus: in reply. *Neurosurgery, 73*(2), 382-3.

Merigan, W. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience, 16*, 369-402.

Polanen, V. (2015). Interactions between dorsal and ventral streams for controlling skilled grasp. *Neuropsychologia, 79*(Pt), 186-91.

Rossit, S. (2011). Impaired delayed but preserved immediate grasping in a neglect patient with parieto-occipital lesions. *Neuropsychologia, 49*(9), 2498-504.

Roth, Z. N. (2015). Position and Identity Information Available in fMRI Patterns of Activity in Human Visual Cortex. *Journal of Neuroscience, 35*(33), 11559-71.

Saber, G. T. (2015). Saccade planning evokes topographically specific activity in the dorsal and ventral streams. *Journal of Neuroscience, 35*(1), 245-52.

Singhal, A. (2013). Human fMRI reveals that delayed action re-recruits visual perception. *PLoS ONE, 8*(9)

Takemura, H. (2015). A Major Human White Matter Pathway Between Dorsal and Ventral Visual Cortex. *Cerebral Cortex,*

Toth, L. J. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature, 415*(6868), 165-8.

Verhagen, L. (2013). Hierarchical organization of parietofrontal circuits during goal-directed action. *Journal of Neuroscience, 33*(15), 6492-503.

Verhoef, B. E. (2011). Synchronization between the end stages of the dorsal and the ventral visual stream. *Journal of Neurophysiology, 105*(5), 2030-42.

Whitwell, R. L. (2014). The Two Visual Systems Hypothesis: New Challenges and Insights from Visual form Agnosic Patient DF. *Frontiers in Neurology, 5*

Zanon, M. (2010). Cortical connections between dorsal and ventral visual streams in humans: Evidence by TMS/EEG co-registration. *Brain Topography, 22*(4), 307-17.

Zhong, Y. M. (2003). Inferior parietal lobule projections to anterior inferotemporal cortex (area TE) in macaque monkey. *Cerebral Cortex, 13*(5), 527-40.

Mark F. 2001. Neuroscience, exploring the brain. 4th edition, Lippincott Williams and Wilkins