

11 Moving and Being Moved: The Importance of Dynamic Information in Clinical Populations

B. de Gelder and J. Van den Stock

In encountering a person, what we are most easily conscious of is that their face gives us access to the person's identity. At the same time, the face provides many other kinds of information, such as gender, age, emotional expression, attractiveness, trust, and the like. It is likely that some kinds of information are relatively better conveyed by moving than by static faces. Some of these typical face attributes, for example, identity or affect, are also conveyed by other stimuli than faces, for example, whole bodies. And as is the case with faces, they may be conveyed by a still image as well as by its dynamic counterpart. Thus the relative importance of dynamic information is not an issue restricted to face recognition but is encountered just as well in investigations of object recognition in general.

It has been discussed that faces might be "special" as a set of visual stimuli. Likewise, one might ask whether the processing of dynamic information is special in the context of faces. Very few focused comparisons are available to answer this question because this is a challenging task. A proper comparison of face perception and recognition abilities with other object perception and recognition abilities requires comparable task settings for the two stimulus classes (e.g., Damasio, Tranel, et al., 1990; Farah, 1990). The available comparisons have almost all used still images and this makes it all the more difficult to assess the relative importance of dynamic information for perception of faces.

Face Perception: Some Antecedents

The high salience of faces in everyday life is taken for granted and is reflected in the number of studies devoted to face recognition. Research targeting face recognition got a significant boost from the discovery of face-specific deficits after brain damage reported by Bodamer (1947). Investigations into the functional properties of face processing began with the first neuropsychological studies of Yin (1969), who reported a strong inversion effect for faces, and it has been growing exponentially

since the beginning of brain-imaging studies of face recognition. More and more clinical cases were also reported this past decade, with specific impairments in face recognition abilities. An overview of findings from functional magnetic resonance imaging studies in these clinical cases can be found in Van den Stock et al. (2008) and an overview of EEG studies in Righart and de Gelder (2007).

The combined findings from behavioral, clinical, and neuroimaging studies are integrated in theoretical models of face perception, of which the model of Bruce and Young (1986) has been one of the most influential. Since then, a few other models of face perception have been proposed (e.g., Haxby, Hoffman, & Gabbini, 2000). They have increased our understanding mainly by integrating new findings about face recognition deficits, its neurofunctional basis, category specificity, the relative separation of subsystems like those for identity and expression, genetic basis, the importance of movement information, and the contribution of real-world and context elements. The central notion in contemporary models is that different aspects of face perception, such as identity, expression, and direction of gaze, are processed in a brain network in which the different areas show relative functional specialization.

The neurofunctional basis of processing facial identity in neurologically intact individuals is reasonably well understood. Sergent and Signoret (1992) first described the middle lateral fusiform gyrus (FG) to be responsive to faces. Kanwisher, McDermott, and Chun (1997) later dubbed this region the fusiform face area. The occipital face area is another important face-sensitive area located in the inferior occipital gyrus (Puce et al., 1996). Although these areas have been related to identity processing, the main area that comes into play when the face carries an emotional expression is the amygdala (AMG). The AMG plays a critical role in mediating emotional responses and actions (see Zald, 2003, for a review). Several studies support the notion that activity in the FFA increases as a result of feedback from the AMG (e.g., Breiter et al., 1996) and anatomical connections between the amygdala and the visual cortex have been established in primates (Amaral & Price, 1984). Faces expressing emotions also modulate OFA activity (Rotshtein et al., 2001). On the other hand, AMG-driven threat-related modulations also involve earlier visual areas such as V1 and other distant regions involved in social, cognitive, or somatic responses (e.g., the superior temporal sulcus [STS], cingulate, or parietal areas) (Catani et al., 2003). The rapid activity and/or the involvement of posterior visual areas in normal persons have been related to coarse processing of salient stimuli in subcortical structures. Support for subcortical processing of salient stimuli of which facial expressions are an example is also provided by residual face perception in patients with striate cortex lesions (Morris et al., 2001).

The Brain Basis of Face Perception in Neurologically Intact Individuals: Perceiving Movement

It needs no stating that in daily life the faces we perceive and interact with are almost continuously in motion and our perceptual systems therefore have more experience with dynamic than with static faces. The movements generated by the complex musculature of the face or body make a substantial contribution to nonverbal communication. Moreover, there are several characteristics of a person that are almost exclusively revealed by the dynamic properties displayed in the face or body: looking at a photograph of Marlon Brando playing Don Corleone in the *Godfather* results in an experience quite different from that of watching his live performance in the scene in which he addresses the heads of the families. This difference is illustrative of the clear additive value that lies in the temporal unfolding of dynamic facial expressions.

Before developing this point though, it is worth mentioning that using still images to probe face processing may have unique advantages in probing the neurofunctional basis of processing in normal as well as in neurological patients. Static patterns get the mind moving as the brain processes the incoming still image by actively mapping it onto a representation that incorporates the movement and the temporal dynamics normally associated with this visual stimulus in the external world. Well-known studies by, e.g., Shepard & Zare (1983) and by Freyd (1983) have shown convincingly that still images can be fruitfully used to probe movement perception in the brain. Using still images of whole-body expressions, we observed activation in brain areas that are normally sensitive to movement, such as the STS in human observers (de Gelder et al., 2004) and in macaques (de Gelder & Partan, 2009).

Although the importance of dynamic expressions and their interpretation by conspecifics has long been recognized in the animal literature (Dawkins & Krebs, 1978), it is quite surprising that there are still only a few neuroimaging investigations with neurologically intact participants that used dynamic expressions. The dynamic information in facial expressions represents a specific kind of biological motion (Johansson, 1973). Therefore it is reasonable to expect that perceiving facial and bodily movements will activate areas known to be involved in movement perception, such as the hMT/V5 complex, and in perception of socially relevant movement, such as the STS (Bonda et al., 1996). Furthermore, socially relevant and emotionally laden movement is likely to involve the AMG.

A few studies throw light on these issues, but many open questions remain. For example, it is not known whether the neurofunctional basis of biological movement in faces and bodies is a special case of the more general ability for processing biological as contrasted with nonbiological movement. Alternatively, facial movement patterns that are specifically at the service of facial expressions may be a *sui generis* specialization of the brain that only minimally overlaps with the neurofunctional

mechanisms sustaining perception of biological movement in general. The former possibility evokes the notion of a specialized speech module exclusively at the service of the analysis of visual speech. Liberman and colleagues (see Liberman, 1996) developed the argument for such an analysis model for phonetic gestures in the seventies and eighties. A review of the pro and con arguments is provided in the volume dedicated to Al Liberman.

More recently, this approach to speech has been viewed as an example of action perception by researchers in the field of mirror neuron-based perception of action. However, once relatively complex stimuli are considered, it remains unclear so far what the relation is between movement and action perception and execution (Pichon et al., 2009). Furthermore, the motor theory of speech perception was motivated by the ambition to start from but reach beyond the available linguistic description of phonetic features and define the set of motor primitives that may be the basis of speech perception. Neither for the more general case of biological movement, nor for the specific ones of human facial movements do we have descriptive theories available at present. Studies of mirror neuron activation have so far been restricted to individual single actions that do not yet allow insight into action primitives. Possibly the analysis of facial motor patterns (the FACS, facial action coding system; Ekman & Friesen, 1978) and bodily emotional motor patterns (BACS, body action coding system; de Gelder & van Boxtel, 2009 [internal report]) that implement emotional expressions may provide input for a future theory of emotional movement primitives.

With these caveats in mind, let us turn to available research. In a positron emission tomography study by Kilts, Egan, Gideon, Ely, & Hoffman (2003), participants were presented with angry, happy, and neutral facial expressions and nonface objects that were either static or dynamic. The perception of dynamic neutral faces, compared with dynamic nonface objects, triggered activity in the AMG, STS, and FG, but none of these areas were active when dynamic neutral faces were compared with static neutral faces. However, dynamic angry faces elicited more activity in these areas than static angry faces. This highlights the importance of emotional information conveyed by facial expressions in a comparison of dynamic and static faces. The increased recruitment of the AMG, STS, and FG in dynamic facial expressions might be specific for expressions with a negative valence since there was no difference in these areas between dynamic and static displays of happy faces.

Similar findings are reported with fMRI data; dynamic facial expressions (neutral, fear, and anger) yielded more activity than static emotional faces in the AMG and FG (LaBar, Crupain, Voyvodic, & McCarthy, 2003). An overview of currently available functional imaging studies with dynamic facial expressions is given in table 11.1. The general findings show that comparisons between dynamic faces and

Table 11.1
Functional imaging studies with dynamic facial expressions

	Method	Stimuli	Task	Contrast	AMG	FG	STS	OFA
Kilts (2003)	PET	FneuD FangD FhapD FneuS FfeaS FangS nonFD nonFS	Emotion intensity rating	FneuD > DnonF FneuD > FneuS FangD > FangS FhapD > FhapS	X X	X X	X X	 X X
LaBar (2003)	fMRI	FneuD FangD FfeaD FneuS FfeaS FfeaS	Category classification	FneuD > FneuS FemoD > FemoS FangD > FangS FfeaD > FfeaS	X X X	X X X X		
Puce (2003)	fMRI	FneuD FneuD(l) nonFD	Passive viewing	[FneuD + FneuD(l)] > nonFD		X	X	
Decety (2003)	PET	FneuD ¹ FhapD ¹ FsadD ¹	Mood rating	FhapD > FneuD FsadD > FneuD				
Wicker (2003)	fMRI	FneuD FdisD FhapD	Passive viewing	FdisD > FneuD FhapD > FneuD		X X	X	X
Sato (2004)	fMRI	FfeaD FhapD FfeaS FangS nonFD	Passive viewing	FfeaD > FfeaS FfeaD > nonFD FhapD > FhapS FhapD > nonFD	X X	X X X X	X X X X	X X X X
Wheaton (2004)	fMRI	FneuD FneuS	Passive viewing	FneuD > FneuS		X	X	
Grosbras (2006)	fMRI	FneuD FangD nonFD	Passive viewing	FneuD > nonFD FangD > nonFD	X X	X X	X X	X X
van der Gaag (2007a)	fMRI	FneuD FdisD FfeaD FhapD	Passive viewing	FallD > R	X	X		
van der Gaag (2007b)	fMRI	FneuD FdisD FfeaD FhapD nonFD	Passive viewing Discrimination	FallD > nonFD FallD > nonFD	X ² X ²			
Thompson (2007)	fMRI	FneuD(s) nonFD	Speed change detection	FneuD > nonFD			X	

Table 11.1
(continued)

	Method	Stimuli	Task	Contrast	AMG	FG	STS	OFA
Kret (2009)	fMRI	FangD FfeaD FneuD BangD BfeaD BneuD	Oddball detection	FallD > BallD FemoD > FneuD	X	X	X	

Notes: D, dynamic; S, static; Fang, angry face; Fdis, disgusted face; Ffea, fearful face; Fneu, neutral face; Fhap, happy face; Femo, emotional face; Fall, all faces; nonF, non-face; R, rest; (s), synthetic; (l), line drawing; Bang, angry body; Bfea, fearful body; Bneu, neutral body; Ball, all bodies.

¹The conditions reported involve the motoric expression of the stimuli, not the semantic content of the stories told by the actor.

²No modulation of AMG activity by emotional content of faces.

dynamic nonface stimuli typically activate brain areas already known to be involved in the perception of static faces. Taken at face value, this result suggests that the difference in brain basis between seeing still and dynamic faces is quantitative rather than qualitative. However, a more focused comparison between dynamic and static faces shows a less clear picture, and the contrast becomes stronger when emotional expressions are part of the comparison.

In a recent study we investigated the neural correlates of perceiving dynamic face images using a design built on a close comparison of face videos with body videos. To arrive at a better view of dynamic neutral versus emotional (fearful and angry) facial expressions, we used both categories and compared each with its counterpart (Kret, Grezes, Pichon, & de Gelder, submitted). The face versus body comparison showed activation in the AMG and hippocampus. Dynamic emotional faces yielded more activity in the FG and STS than dynamic neutral faces. We found no emotional modulation of the AMG by dynamic emotional compared with neutral faces, a result that is consistent with a study that focused on amygdala activation (van der Gaag, Minderaa et al., 2007a).

Neurophysiological Studies in Monkeys

Single-cell recordings in monkeys have shown that cells in the inter temporal cortex and the STS are responsive to different aspects of face perception (e.g., Bruce, Desimone, & Gross, 1986), including emotional expression (Hasselmo, Rolls, & Baylis, 1989). However, the use of dynamic face stimuli in neurophysiological monkey studies is rare. Evidence exists of neurons that are sensitive to specific movements of the head (Hasselmo, Rolls, & Baylis, 1989) and dynamic whole-body expressions (Oram

& Perrett, 1996). One neurophysiological study reported neurons in the monkey STS that are sensitive to facial dynamics like closing the eyes (Hasselmo, Rolls, & Baylis, 1989). Other cells have been described that are sensitive to threatening open mouths (Perrett & Mistlin, 1990).

Similarly in humans, the STS was found to be active following social information when dynamic images were used (see table 11.1). Neurons in the amygdala have also been reported to be responsive to social information in monkeys (e.g., Brothers, Ring, & Kling, 1990).

Visual Object Agnosia and Face Agnosia or Prosopagnosia

Prosopagnosia was first reported by Bodamer (1947). The deficit involves recognition of personal identity but not of facial expression. This dissociation has been the cornerstone of the models of face processing in the neuropsychological literature of the past two decades and is at the basis of the face recognition model of Bruce and Young (1986). The typical complaint of a prosopagnosic is the inability to recognize a person by their face. This symptom is far more pronounced than the phenomenon everyone sometimes experiences when they have trouble remembering from where or how they know a certain face. Prosopagnosics can even have difficulties recognizing the persons they are very close to, such as their immediate family members.

Neural Correlates of Face Deficits

The focus on finding the neural correlate of the physically defined face category raised the expectation that patients with face recognition deficits would show lesions or anomalous activation in the normal face recognition areas. This has not always turned out to be the case, as shown by some recent patient studies using brain imaging (e.g., Steeves, Culham, Duchaine, Pratesi, Valyear, et al., 2006). When we turn to developmental prosopagnosia (DP), the situation is not clearer. Investigations into the neurofunctional correlates of DP with fMRI have yielded inconsistent results. Several studies reported increased activity for perceiving faces, compared with non-face stimuli, in the well-known face areas FFA and OFA (e.g., Hasson, Avidan, Dunhill, Berton et al., 2007) whereas the first fMRI study including a DP case by Hadjikhani and de Gelder (2002) and a more recent study (Bentin, Degutis, D'Esposito, & Robertson, 2007) found no face-specific activation in these areas. These findings suggest that intact functioning of the FFA and inferior occipital gyrus are necessary but not sufficient for successful face recognition.

An important issue concerns the emotional information contained by the perceived faces. Recently, we observed reduced activation levels in the FFA of three

developmental prosopagnosics compared to control subjects when looking at neutral faces. However, there was no difference between both groups in the activation level of the FFA when the faces they viewed expressed either a happy or a fearful emotion (Van den Stock, van de Riet, Righart, & de Gelder, 2008). In the same study, we investigated the neural correlates of perceiving neutral and emotional whole-body expressions and the results showed that in prosopagnosics, the perception of bodies is associated with increased activation in face areas and the perception of faces elicits activity in body areas. Whole-body expressions are quite eligible as a control stimulus condition for faces since they are comparable to faces on a number of variables, for instance, ability to express emotional information, gender, age, or familiarity.

Still versus Dynamic Face Images in Patient Studies

Impairments in recognizing emotion or identity in facial expressions have been reported in a variety of syndromes like Huntington's disease (Sprengelmeyer et al., 1996), Wilson's disease (Wang, Hoosain, Yang, Meng, Wang, 2003), Urbach-Wiethe disease (Adolphs, Tranel, Damasio, & Damasio, 1994), Parkinson's disease (Sprengelmeyer, Young, et al., 2003), autism spectrum disorder (for a review, see Sasson, 2006), obsessive-compulsive disorder (Sprengelmeyer, Young, et al., 1997), schizophrenia (Mandal, Pandey, & Prasad, 1998, for review), Alzheimer's disease (Hargrave, Maddock, & Stone, 2002), semantic dementia (Bozeat, Lambon Ralph, Patterson, Garrard, Hodges, 2000), attention deficit hyperactivity disorder (Singh, Ellis, Winton, Singh, Leung, 1998), amyotrophic lateral sclerosis (Zimmerman, Eslinger, et al., 2007), and frontotemporal dementia (Lavenex, Pasquier, Lebert, Petit, & van der Linden, 1999). However, the bulk of these studies are based on the use of static stimuli, and recognition of static facial expressions calls for a larger effort of the brain than dynamic expressions since the brain has to account for the missing information of temporal dynamics. It is therefore not surprising that several studies with patients found superior recognition of dynamic facial expressions compared with static expressions (Tomlinson et al., 2006). One study with a prosopagnosic reported impaired identity recognition of static face pictures, but not of dynamic faces (Steede, Tree, et al., 2007), a pattern that was not compatible with a similar previous study (Lander, Humphreys, & Bruce, 2004).

As far as recognition of facial speech expressions is concerned, we tested a patient with prosopagnosia using still images of facial expressions as well as dynamic videos (de Gelder & Vroomen, 1998). Her performance with still facial expressions was poor but improved significantly when short videos were shown instead. The same pattern was observed in another prosopagnosic patient using point-light displays of emotional face expressions (Humphreys, Donnelly, & Ridloch, 1993).

Being Moved by Still Images

It is often assumed that dynamic stimuli are easier to decode than still images, and the most frequent argument is that dynamic images are more natural or more ecological and thereby more representative of the visual input the brain has evolved for. As we already pointed out, comparisons are complicated by the simple fact that dynamic stimuli contain much more information than still images. On the other hand, there are arguments about the specificity of movement perception that speak against a simple comparison that takes the higher information content of dynamic images into account. One of these is the fact that there are known cases in the neuropsychological literature of movement perception disorders. One of the best ones is Zihl's patient with bilateral lesions to V5. This patient had a severe movement perception deficit but had no difficulty in recognizing people by their faces and was not prosopagnosic. She was also able to read speech from static face images but could not perceive speech from dynamic images (Campbell, Zihl, Massaro, Munhall, & Cohen, 1997). The reverse pattern was observed in a patient with lesions in V4 (Humphreys, Donnelly, & Riddoch, 1993).

A convergent argument to which we have already alluded several times in favor of a nuance in the distinction between still and dynamic images is that studies using still images have reported activation in motor and premotor areas. This clearly means the brain does not need to be shown movement in order to perceive it. As a matter of fact, using still images may provide a tool for assessing the brain's perceptual abilities beyond the strictly physically present information.

Face Perception in Hemianope Patients

Of particular interest for understanding the neurofunctional basis of perceiving facial movement are patients with damage to the primary visual cortex. Previous studies of such rare cases have illustrated the extent of residual movement vision that does not depend on an intact V1. It is interesting that movement perception with versus without awareness is correlated with different stimulus properties (for review Weiskrantz, 2009).

In our first investigation of the residual vision of hemianope patients, we used both still images and short video clips of faces and we found that only the video clips triggered a reliable recognition of facial expressions in the blind field. This suggested that the presence of movement may be a necessary condition for affective blindsight (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). However, in subsequent studies we used EEG and later fMRI measurements and found clear evidence that still images were also processed (e.g., Rossion, de Gelder, Pourtois, Guérit, &

Weiskrantz, 2000). Returning to a more sensitive behavioral paradigm than direct guessing by using the redundant target effect based on the advantage derived from summation across the two hemifields, here the sighted and the blind one, we showed later that still face images are still reliably recognized (e.g., de Gelder, Pourtois, Weiskrantz, 2002). In a recent study we report that the presence of still facial and bodily images triggers muscular movements that can be measured by electromyography. These facial movements reflect the specific emotion expressed in the unseen stimulus, independently of whether it is a face or a body, and have shorter latencies when triggered by an unseen than by a seen stimulus. However, at no time are the subjects aware of the unseen stimulus or of their motor reaction to it (Tamietto et al., submitted).

Conclusion

The human perceptual system is eminently tuned to information provided by movement in the environment. The corollary of this is that when it is dealing with still images, the brain will automatically represent the dynamic information that is not, strictly speaking, present in the stimulus. Perceptual deficits, either congenital or as a consequence of brain damage in the normally developed brain, challenge our current understanding of the neurofunctional basis of movement perception. On the one hand there is little doubt that moving images provide more and richer information that, other things being equal, may make it easier for brains and perceptual systems weakened by disease to access information. On the other hand, there is also little doubt that in the developed brain a certain division of labor underpins fluent perceptual abilities. To approach this neuronal division of labor as exclusively a matter of specialized face, movement, or emotion modules may hamper our understanding of these perceptual abilities and the active role of the perceptual system in dealing with stimuli.

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