Understanding Other People Through Perception of Human Social Actions: From Action Recognition to Social Interaction

Dissertation

zur Erlangung des Grades eines
Doktors der Naturwissenschaften

der Mathematisch-Naturwissenschaftlichen Fakultät
und der Medizinischen Fakultät
der Eberhard-Karls-Universität Tübingen

vorgelegt
von

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aus Heidelberg, Deutschland

Juni 2016

Tag der mündlichen Prüfung: 21. Juli 2016

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Dong-Seon Chang

Acknowledgements

- I want to thank Dr. Stephan de la Rosa for his steady support and great supervision, being always so patient and helping me to go through many difficult phases during my PhD work.

- I want to express my gratefulness to Prof. Dr. Heinrich H. Bülthoff for giving me the opportunity to work at such an outstanding research institute, with great colleagues, and state-of-the-art technologies, the Max Planck Institute for Biological Cybernetics in Tübingen, Germany, will always be in my memories.

- I would also like to thank all my advisors from my advisory board, Prof. Dr. Dr. Kai Vogeley, Prof. Dr. Martin Giese, and Dr. Hong Yu Wong, for their consistent support, useful comments and fruitful discussions of my work.

- Many thanks also to the administration, Dagmar Maier, and the system administrators, Walter Heinz and Timo Hertel, as well as all the technicians of the institute, Joachim Bieg, and Michael Kerger, only their constant invisible help made many things possible.

- I also thank former and current members of the Social & Spatial Cognition Group and RECCAT Group for their great discussions, help and support: Stephan Streuber, Christian Wallraven, Tobias Meilinger, Isabelle Bülthoff, Janina Esins, Katharina Dobs, Trevor Dodds, Aurelie Saulton, Laura Fademrecht, Thomas Hinterecker, Marianne Strickrodt… - and Frank Drop, with whom I was PhD representative for nearly 2 years together, and Stefano Geluardi, who is the lovely godfather of my son Theo. - I also want to also thank all colleagues at my institute, who I will not name one by one, but who made my time at the institute enjoyable.

- Last, but not at least, I want to thank my beloved wife Eugene the most, for the incredible patience and support, for staying with me in a totally foreign country, throughout all the years I was working on my PhD thesis. Thank you and love you.

Summary

How do we understand the actions of other people? Understanding other human beings is one of the most challenging tasks for the human brain. Although humans have evolved into highly social animals equipped with remarkable capacities to achieve effortless interaction with each other, the underlying brain mechanisms enabling us to observe, act, and predict the behavior of other humans are still largely unknown.

The current PhD thesis attempts to advance our knowledge about how we understand other humans by investigating perception and recognition of human social actions in various different contexts. The first study (Chapter 2) tries to investigate how the brain discriminates between different social actions using a visual adaptation paradigm, and compares kinematic and semantic similarities between different action pairs. The second study (Chapter 3) compares the processes underlying action recognition between different cultures – namely Germany and Korea. The third study (Chapter 4) asks the question whether we use shared representations of actions to encode complementary actions occurring in everyday life social interactions. The last study (Chapter 5) examines how we perceive the actions of an interaction partner if we are physically coupled together with a rope, but cannot see or hear the partner. Taken together, the current PhD work aims to study the underlying mechanisms of social cognition by various methods – from action recognition studies using visual adaptation paradigms to more complex studies of social interactions with direct and observed pairwise interactions.

The results of the current work reveal that (1) both kinematic and semantic components play an important role for the encoding of action representations, (2) action recognition processes are surprisingly robust and consistent across different cultures, (3) action representations are shared for complementary actions in social interactions, and (4) humans perceive social information from actions even in situations with minimal possibilities for communication. In summary, the current work provides new insights into the brain mechanisms how humans understand other people through the perception and recognition of social actions inside and outside of social interactions.

”The dangerous man is the one
who has only one idea,
because then he’ll fight and die for it.
The way real science goes is
that you come up with lots of ideas,
and most of them will be wrong.”

- Francis Crick quoting Linus Pauling, 1995 [*]

Prudens quaestio, dimidium scientiae

– To know what to question is to know half already.

- Francis Bacon quoting Aristotle, 1620 [#]

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[*] Francis Crick, “The Impact of Linus Pauling on Molecular Biology”, 1995, The Pauling Symposium, Oregon State University;
Exact passage quoted from The New Yorker, 25. 04.2011

[#] Francis Bacon, “Novum Organum Scientiarum”, 1620/1878, Clarendon Press, Oxford;
Exact passage quoted from LIFE Magazine, 08. 09.1958

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1

Synopsis

Imagine you are an alien who just arrived on earth. You are here to study the behavior of a particular species: *Homo Sapiens*. You do not know anything about this bewildering organism, how it functions and how it survives in its environment. What would be your first questions to start investigating this species? What potential conclusions could you draw from just “observing” the behavior of humans, without really “being” human?

The ways scientists try to figure out how humans understand other humans and their actions are somewhat similar to the problem in this example. We cannot really explain how we manage to understand other people’s minds, how we predict their behaviors, and how we process information about other individuals by ourselves. As the philosopher Michael Polanyi has pointed out already in 1966, “We can know more than we can tell (…) The skill of a driver cannot be replaced by a thorough schooling in the theory of the motorcar; the knowledge I have of my own body differs altogether from the knowledge of its physiology.” (Polanyi, 1966) In other words, although we have a certain implicit knowledge by ourselves (because we are humans) we would not be able to teach a machine or robot how we function as humans and we would certainly not be able to explain this to aliens yet, if we were to ever meet them.

The first question, any investigator of human behavior might ask, however, starts most certainly with the **problem of perception**: How do we humans understand the physical world? How do we interpret the abundancy of signals in our environments conveyed to our brains and give meaning to them?

Based on the advances in the fields of experimental psychology and evolutionary biology since the launch of the field of psychophysics (Fechner, 1877), most perceptual scientists would agree that the principle of natural selection and evolution has shaped our sensory systems to accurately estimate the signals in our environment (Hoffman, Singh, & Prakash, 2015). Especially for humans, the visual system has evolved to play the most important role in decoding information from the environment. This idea has been nicely put into words by David Marr:

> "Vision is a process that produces from images of the external world a description that is useful to the viewer and not cluttered with irrelevant information."
> (Marr, 1982)

This fundamental idea that perception is always based on assumptions about the world relevant for survival, and closely coupled in interaction with its environment, has been further put forward by Alan Yuille and Heinrich Bülthoff:

> "The brain, or any artificial vision system, must make assumptions about the real world. These assumptions must be sufficiently powerful to ensure that vision is well-posed for those properties in the scene that the visual system needs to estimate."
> (Yuille & Bülthoff, 1996)

But out of all the signals in the real world, which ones would possess the most immediate and relevant properties needed to estimate? According to a broad range of findings from multiple science disciplines, the most salient and important signals for humans seem to be those ones generated by their conspecifics: Other humans (Adolphs, 1999, 2001, 2009; Frith & Frith, 2007, 2012; Lieberman, 2007; Saxe, 2006; Seyfarth & Cheney, 2015; Tomasello, Carpenter, Call, Behne, & Moll, 2005a; Tomasello, 2014).

1.1. The Social Brain: Why do we care about other humans?

What makes the perception of social signals from other conspecifics so special for the human brain? While we humans are inherently social animals adapted to living in groups, we also share a lot of neurobiological and psychological mechanisms with other group-living animals (Adolphs, 2009). These mechanisms include not only similar group dynamics (Conradt & Roper, 2005; Couzin, 2009; Dyer, Johansson, Helbing, Couzin, & Krause, 2009), but also various modes of social learning, observing and tracking other individuals' behavior and interactions, and acknowledging other individuals' social relationships (Cheney & Seyfarth, 1990; Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, Seyfarth, & Cheney, 2007; Seyfarth & Cheney, 2012, 2015; Silk, 2007).

However, it has been pointed out that not only the degree to which humans can infer the knowledge, beliefs and intentions of other humans, but also the dimensions of complexity in social organization, and the abilities to cooperate and coordinate actions with each other is extraordinary and unprecedented in the animal world (Herrmann, Call, Hernàndez-Lloreda, Hare, & Tomasello, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005b; Tomasello, 2011, 2014; Warneken, Chen, & Tomasello, 2006). In other words, humans are truly specialized to perceive and interpret social signals from other humans (Adolphs, 2009; C. D. Frith & Frith, 2007; Lieberman, 2007; Saxe, 2006; Spelke, Bernier, & Skerry, 2013).

There are at least three major arguments counting as evidence for why our human brain is essentially specialized for social signals:

The first is called the “Social Brain Hypothesis” and comes from the findings of evolutionary anthropology and biology demonstrating a quantitative relationship between brain size, especially the size of the neocortex, and social group size (Dunbar, 1998a, 1998b, 2003; Kudo & Dunbar, 2001). This theory states a fundamental relationship between the cognitive demands of social complexity and the human evolution of intelligence.

The second argument is called the “Cultural Intelligence Hypothesis” and comes from the findings of evolutionary anthropology and developmental psychology, showing that even human children possess species-specific sets of social skills which do not show up in other species such as ‘mindreading’ and ‘shared intentionality’ which are probably due to specializations of the human brain for cultural cognition throughout evolution (Herrmann et al., 2007; Tomasello et al., 2005a). This argument is accompanied by a number of slightly different variations each emphasizing different social reasons for the development of intelligence, e.g. “Social Intelligence Hypothesis” (Humphrey, 1976) and “Machiavellian Intelligence Hypothesis” (Whiten & Byrne, 1988) focusing on human competition, and “Vygotskyan Intelligence Hypothesis”(Moll & Tomasello, 2007) emphasizing human cooperation.

The third argument is coming from recent findings in the fields of cognitive neuroscience and neuroimaging investigating the “Default Mode Network” in the brain. Recent studies show that areas in the brain which are typically more active during rest than during active task performance are largely overlapping with brain networks processing social information (Mars et al., 2012; Raichle & Snyder, 2007; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008). These results have been interpreted as evidence how humans have a predisposition for the processing of social information as the default mode of perceptual inference (Schilbach et al., 2008).

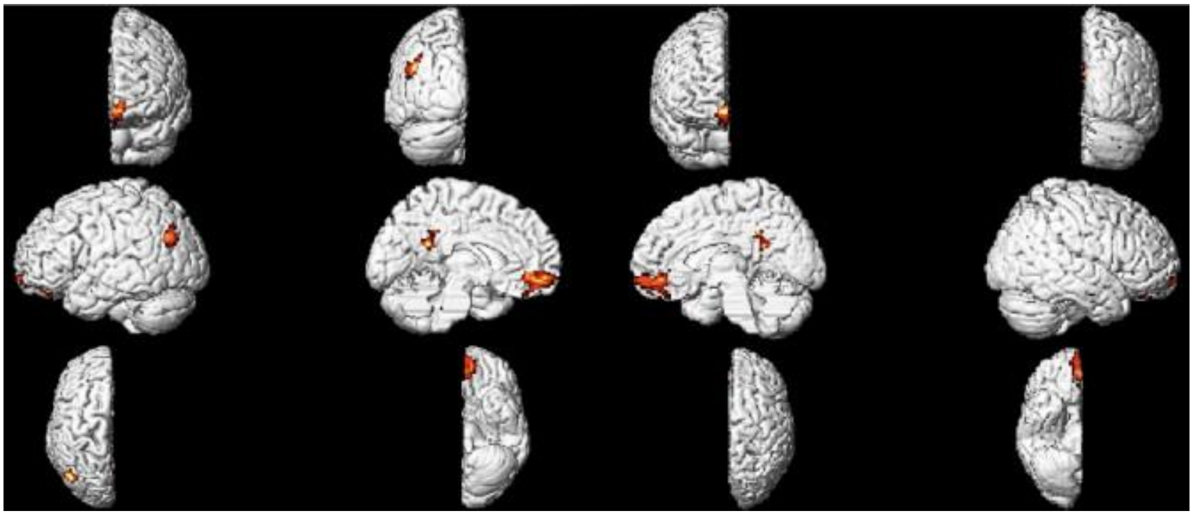

Figure 1-1. Neural overlaps between the Default Mode Network and the correlates of social cognition network
The neural correlates of conjunction analysis across 12 neuroimaging studies are shown.
Adapted from Schilbach et al., 2008

Taken together, we can summarize that the reason why we as humans care so much about the activities of other humans lies in the history of evolution of the human brain: By the demands to deal with other humans and predict their thoughts and behaviors, our brains have evolved to become a truly "social brain", specialized for other humans. Although this question can also be asked from both ways: "Did the general demands for greater cognitive abilities and intelligence drive our brains to become social, or did the social brain enable us humans to reach greater intelligence?" (Adolphs, 2009; Roth & Dicke, 2005) it is undeniable that social information processing plays an important role for the human brain.

1.2. Social Cognition: Understanding Other People

Social cognition is about understanding other people (Lieberman, 2007), and encompasses generally all processes that enable humans to interact with other humans (Adolphs, 1999). This implies that the main goal of this field of research is to study how people process social information in various situations (Frith & Frith, 2007).

1.2.1. Processes underlying Social Cognition: What do we know about other humans?

Latest advances in fields of cognitive psychology and social neuroscience have helped us to distinguish roughly between two sets of processes underlying social cognition:

Automatic	**vs.**	**Controlled**	(Adolphs, 2009, 2010)
Implicit	**vs.**	**Explicit**	(Frith & Frith, 2008, 2012)
Reflexive	**vs.**	**Reflective**	
(X-system	**vs.**	**C-system)**	(Lieberman, 2007, 2010)

The former processes – automatic, implicit, reflexive – encompass a broader range of phenomena in social life, since a number of situations in real life social interactions require relatively fast and spontaneous reactions to social stimuli without conscious awareness. Therefore, many processes involved in social cognition are known to be automatic or implicit (Frith & Frith, 2008), typically including the following examples: Gaze following, Action imitation / Action mimicry, Judgments of other people's personal attributes (Thinslicing). These processes help us coordinating our actions with other people (Gaze following → Joint attention), building relationships (Mimicry → Empathy), and interacting in groups (Thinslicing → Teambuilding) (Bar, Neta, & Linz, 2006; Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004; Frischen, Bayliss, &

Tipper, 2007; Hamilton, Brindley, & Frith, 2007; Sebanz & Knoblich, 2009; Willis & Todorov, 2006; Yoon & Tennie, 2010).

The latter processes – controlled, explicit, reflective – in social cognition seem to be necessary when one needs to overcome biases through conscious, deliberate top-down control. For example, these deliberate processes help in racial biases, and prejudices and stereotypes against particular social groups. Moreover, these deliberate processes are indispensable in situations of teaching and learning, especially when verbal instructions via language are necessary (Frith & Frith, 2012; Zaki, Hennigan, Weber, & Ochsner, 2010; Zaki & Ochsner, 2009). In addition, metacognitive processes – consciously reflecting about one's own cognitive processes – also play an important role in human social interactions as well as for the transfer of cultural knowledges.

However, recent findings also acknowledge that this dichotomy between automatic and controlled processes is not always so strict, and a third category might exist linking both processes (Adolphs, 2009). Furthermore, processes such as 'mentalizing' are known to happen both implicitly (in normal subjects) and explicitly (e.g. in high-functioning autism disorder patients) (Frith & Frith, 2008).

Social signals involved in social cognition can also be categorized into different domains based on their medium of transmission, for example, via:

Face: Identity, Age, Gender, Ethnicity, Emotional expressions …

(Haxby, Hoffman, & Gobbini, 2000; Kanwisher, 2000; Tsao & Livingstone, 2008)

Body: Identity, Gender, Ethnicity, Emotional expressions …

(de Gelder, de Borst, & Watson, 2015; Peelen & Downing, 2007; Tsakiris, 2010)

Actions: Identity, Personality, Intentions, Emotional expressions …

(Blake & Shiffrar, 2007; Giese & Poggio, 2003; Giese & Rizzolatti, 2015)

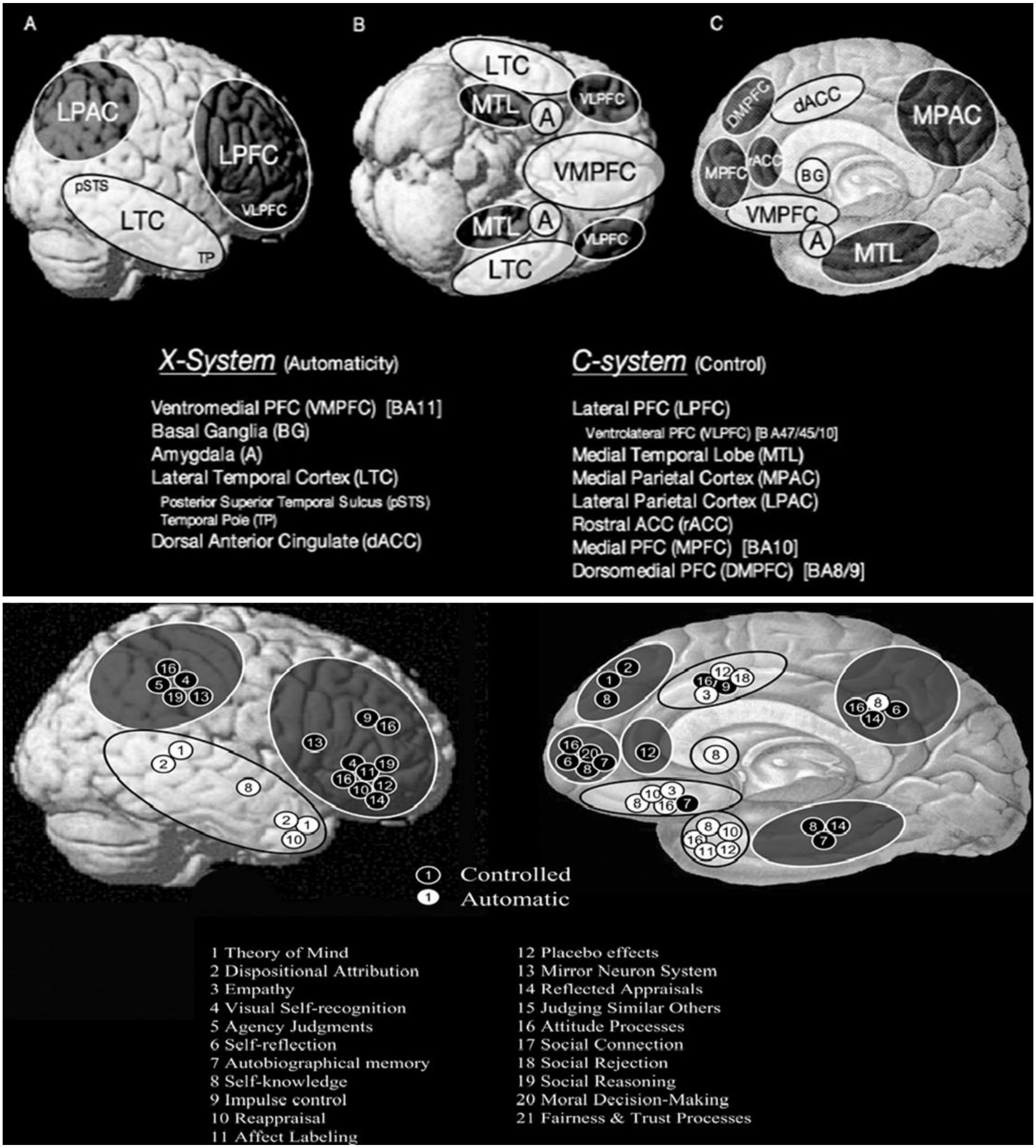

Figure 1-2. Overview of hypothesized brain areas involved in automatic and controlled processes for social cognition: Adapted from Lieberman, 2007

1.2.2. Theories of Social Cognition: How do we know about other humans?

There are currently three major theories trying to give a coherent theoretical account of how we understand other people (Adolphs, 2006; Frith & Frith, 2012; Michael, 2011; Newen, 2015):

The two dominant theories which have been mainly debated over the past few decades are called "Theory Theory (of mind)" and "Simulation Theory (of mind)"(Gallese, Keysers, & Rizzolatti, 2004; Keysers & Gazzola, 2007).

The **"Theory Theory"** claims that each human person holds a basic, naive understanding of the mental states of others, enabling us to make inferences about the beliefs, desires or intentions of other humans (Fodor, 1983, 1992; Frith & Frith, 2006). This ability to make inferences about the mental states of others have been first coined for chimpanzees as "having a theory of mind" (Premack & Woodruff, 1978), and the process of making inferences have been called "mentalizing" (Frith & Frith, 2006; Frith & Frith, 2003).

The **"Simulation Theory"** claims that we understand other humans via simulation mechanisms in ourselves, whereas there could be both low-level and high-level mechanisms (Gallese & Goldman, 1998; Goldman, 2006; Rizzolatti & Sinigaglia, 2010). This theory has been put forward by proponents of the "mirror neuron theory" claiming more concretely that the human brain's motor system is directly involved in the simulation process via 'motor simulation' (Gallese & Goldman, 1998; Gallese et al., 2004; Rizzolatti & Sinigaglia, 2010).

Recent neuroimaging studies have demonstrated that two different, non-overlapping neuroanatomical systems are involved in the process of understanding other humans' minds, whereas the "mentalizing system" has been more closely associated with the "Theory Theory" account and the "mirror system" with the "Simulation Theory" account (Van Overwalle & Baetens, 2009).

A third theoretical account generally called the **“Interaction Theory”** has been only recently added to the discussion, claiming that social interaction is substantial for our understanding of other humans (De Jaegher, Di Paolo, & Gallagher, 2010; Gallagher, 2015; Gallotti & Frith, 2013; Hari, Henriksson, Malinen, & Parkkonen, 2015; Hari & Kujala, 2009; Michael, 2011; Schilbach et al., 2013). Interestingly, the core idea seems to have been lying around in different cultures, since the psychologist Lev A. Vygotsky has claimed already in 1931 that “through others we become ourselves”, and a word expressing the same meaning – *Ubuntu;* “a person becomes a person only through other people” – has been already found in the native African Bantu language (Garfield, Peterson, & Perry, 2001; Hari & Kujala, 2009).

The „Interaction Theory” holds that individualistic accounts of social cognition – both “Theory Theory” and “Simulation Theory” – cannot truly describe the dynamic, context-dependent nature of how we interact with other individuals as well as the environment. According to interactionists, social interaction is the default mode how humans use their brain functions and cognitive abilities, and a true understanding of other humans is only possible by observing the dynamic interaction processes between different individuals (Gallotti & Frith, 2013; Hari et al., 2015; Schilbach et al., 2013).

1.2.3. Mechanisms of Social Cognition: How do we learn about other humans?

How can we acquire knowledge about other humans? There are at least three general mechanisms suggested how we learn about other people, according to Chris Frith and Uta Frith (Frith & Frith, 2006, 2007, 2012):

First, we learn about other humans through direct experience. This has been claimed as the most basic way of learning, since already in insects and other lower animals repeated experience leads to a conditioned response (Jessell, 2000; Seyfarth & Cheney, 2015). For humans, direct interaction with other people lead almost automatically to the generation of "first impressions" and subsequent "reputations" based on the outcome of the interaction (Bar et al., 2006; Fehr & Fischbacher, 2004; Fehr & Gächter, 2002; King-Casas et al., 2005; Nowak & Sigmund, 2005; Schiller, Freeman, Mitchell, Uleman, & Phelps, 2009; Tennie, Frith, & Frith, 2010). It has been shown that the human brain assigns different emotional values to other individuals, based on the experience of interactions (Beer & Ochsner, 2006; Ochsner et al., 2004)

Second, we learn about other humans through observation. This seems a common mechanism also for other social animals how they learn from other individuals (Clayton, Dally, & Emery, 2007; Emery & Clayton, 2009; Frith & Frith, 2012). Even without direct interaction, individuals can associate the reputation and social relationships of other individuals by simply observing a third party interaction (Adolphs, 2009; Crockford et al., 2007; Seyfarth & Cheney, 2012, 2015). It has been shown that also animals are able to infer the knowledge of other individuals (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Premack & Woodruff, 1978; Seyfarth & Cheney, 2012), but the degree to which humans can infer the beliefs, desires and intentions of other individuals seem still very unique and extraordinary (Povinelli & Vonk, 2003; Tomasello et al., 2005a).

Third, we learn about other humans through cultural information. This is by far the most special feature of humans, since only humans seem to possess the sophisticated degree of communication being able to transfer knowledge across many generations (Freeman, Rule, & Ambady, 2009; Han et al., 2012; Herrmann et al., 2007; Tomasello et al., 2005a; Vogeley & Roepstorff, 2009). For example, we do not need a direct experience or direct observation of interactions between individuals, but can easily learn about the reputation of other individuals by communicating with other people who have been previously in the interaction (Adolphs, 2009; Delgado, Frank, & Phelps, 2005; Frith & Frith, 2006). Similarly, we can also use our advanced communicative skills using language to transfer knowledge to children to make them learn new things they have not experienced or observed before (Barsalou, 2008; Fitch, Huber, & Bugnyar, 2010; Garfield et al., 2001; Holtgraves & Kashima, 2008; Pulvermüller, Moseley, Egorova, Shebani, & Boulenger, 2014; Seyfarth & Cheney, 2014). Since these kinds of interactions manifest themselves in a certain group of people over a long period of time, cultural information encompasses social values and norms, different meanings to social events, and provides a closed-loop framework for social behavior, communication and interaction from which humans can collectively learn about other individuals belonging to the same group (Han et al., 2012; Vogeley & Roepstorff, 2009).

1.3. Human Social Actions

Charles Darwin already noted that “actions speak louder than pictures when it comes to understanding what others are doing and feeling”(Blake & Shiffrar, 2007; Darwin, 1872). Thus, it is understandable that the topic of action understanding has been quite a popular research theme for many years and quite extensively studied in the past decades (Blake & Shiffrar, 2007; Giese, 2015). The technique of point-light-animation of biological motion, developed by Gunnar Johannson (Johansson, 1973), has been implemented in many studies of human movements in the past decades and led to numerous interesting findings (Barclay, Cutting, & Kozlowski, 1978; Blake & Shiffrar, 2007; Casile & Giese, 2005; Dittrich, 1993; Giese, 2015; Giese & Poggio, 2003; Kourtzi & Shiffrar, 1999; Lange, Georg, & Lappe, 2006; Loula, Prasad, Harber, & Shiffrar, 2005a; Montepare & Zebrowitz, 1993; Prasad & Shiffrar, 2009; Shiffrar, 2011; Thoresen, Vuong, & Atkinson, 2012; Thornton, Rensink, & Shiffrar, 2002; Troje, Westhoff, & Lavrov, 2005; Troje, 2002).

However, the main question how we understand other humans’ social actions have been debated for long time in the shadow of the two classical competing theories in social cognition: “Theory Theory” and “Simulation Theory” (Brass, Schmitt, Spengler, & Gergely, 2007; Kilner & Frith, 2008; Thioux, Gazzola, & Keysers, 2008). With the discovery of mirror neurons this debate became more heated, and over the past years led to the proposition of numerous different theories on action recognition.

1.3.1. Previous Research on Human Action Recognition – A Rough Overview

Action recognition theories have been proposed from vastly different fields of research – encompassing the fields of visual perception, motor control, computational neuroscience, artificial neural networks, Bayesian inference statistics… and different methodologies such as monkey neurophysiology, human neuroimaging, mathematical modeling, computer vision… (for a thorough review, see Giese & Rizzolatti, 2015)

Another recent systematic overview of different action recognition theories have been offered by Gentsch et al., where action recognition theories were categorized into three different families: “Common Coding”, “Internal Models” and “Simulation Theories” (Gentsch, Weber, Synofzik, Vosgerau, & Schütz-Bosbach, 2016).

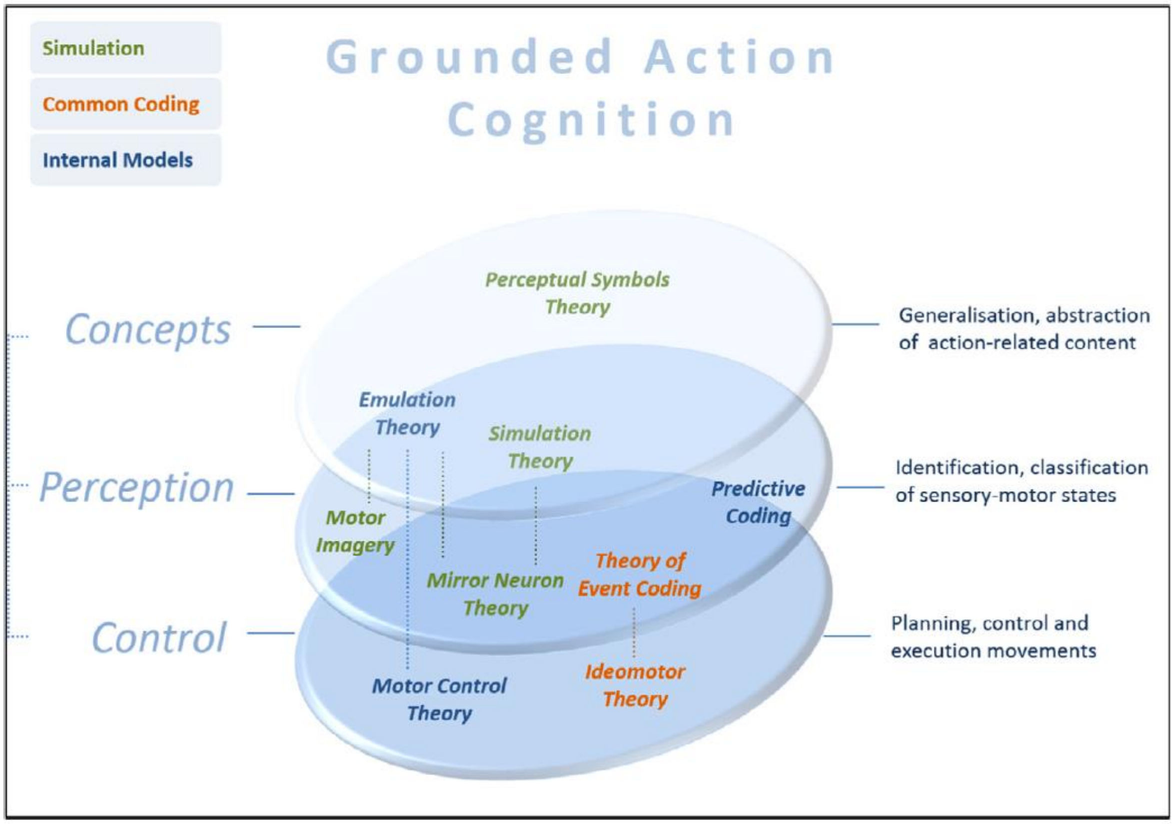

Figure 1-3. Theories of “Grounded Action Cognition” with their main domain of focus. Simulation theories (green) are concerned with action perception and conceptual representations based on mechanisms of motor control. Internal models (blue) mainly describe the relation between motor control and action perception, Common coding (orange) accounts span all three areas of action perception, motor control and concepts. **Adapted from Gentsch et al., 2016**

However, paradigms with a potential to thoroughly examine “action maps in the brain”, or focusing more on the possibility to investigate action recognition in the context of “social interaction” have been mostly lacking.

1.3.2. Visual Action Adaptation Aftereffect Paradigm

Visual action adaptation paradigms offer a great potential to further examine underlying processes to action recognition. Adaptation paradigms have been widely used to examine specific visual recognition processes in the brain (Clifford & Rhodes, 2005; Clifford et al., 2007; Webster, 2011). Visual adaptation is well-known for low-level visual processes such as color, motion or orientation, and recent findings have shown that adaptation even serves a common function for high-level visual recognition processes such as for face identity, face gender, or various social action categories (Armann, Jeffery, Calder, & Rhodes, 2011; Barraclough & Jellema, 2011; Barraclough, Keith, Xiao, Oram, & Perrett, 2009; de la Rosa, Ekramnia, & Bülthoff, 2016; de la Rosa, Ferstl, & Bülthoff, 2016; de la Rosa, Streuber, Giese, Bülthoff, & Curio, 2014; Keefe, Dzhelyova, Perrett, & Barraclough, 2013; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006).

Visual adaptation paradigms possess the following advantages compared to other methodologies:

1) Action adaptation enables measuring the process of action categorization, whereas most other previous methodologies in the field of action recognition just measured reaction time or accuracy for simple action detection tasks.

2) Adaptation paradigms are very robust and consistent with a well visible effect size, so one generally does not need to worry about small effects hidden in the noise of data.

3) Adaptation paradigms enable very specific measures pinning down the underlying neural processes to a specific visual or motor stimulus. This is also very useful to compare the representations to different stimuli within the same categories (Chapter 2).

4) Action adaptation paradigms enable cross-cultural comparisons of perceptual processes by measuring the underlying representations to actions with culturally distinct meanings (Chapter 3).

5) Action adaptation paradigms with multi-player-stimuli enable the measure of action recognition processes in situations of social interaction, or with contingent actions in close spatiotemporal proximities (Chapter 4).

6) Action adaption paradigms with immersive virtual reality (VR) setups enable simulating more realistic social interaction, and can measure the behavior of people in situations more similar to real-life situations (Chapter 4).

7) Action adaptation paradigms enable a comparison of visuo- and motor-processes since both visual and motor adaptation is possible (de la Rosa, Ferstl, et al., 2016).

1.4. Thesis Overview: Aim and Structure of the Thesis

The aim of this thesis was to study how humans understand the action of other people. For this, we employed three different methodologies in our action experiments: A visual action adaptation paradigm, a cross-cultural comparison study, and a dyadic real-time coordination task. These three methodologies were matched to the three different ways we can learn about other people, as suggested previously in the literature, by Frith & Frith (Frith & Frith, 2006):

- Through action observation → Action adaptation study (Chapter 2, 4)
- Through cultural information → Cross-cultural comparison (Chapter 3)
- Through direct experience → Real-time coordination task (Chapter 5)

Previous research on action recognition has been conducted largely in a bottom-up approach by implementing findings from neurophysiological and neuroimaging studies. The studies either focused on the question whether the motor system contributes to the visual recognition of actions (Theory Theory vs. Simulation Theory), or focused only on the question of visual perception how complex movement patterns can be computationally explained by visual pathways covering local motion or form cues (Giese & Poggio, 2003; Lange et al., 2006; Lange & Lappe, 2007; Theusner, de Lussanet, & Lappe, 2014). Although both research directions grew extremely prominent during the past years and have been fruitful in their various findings about action recognition, these findings and models did not yet succeed to explain the representations of high-level, dynamic and context-dependent human social actions in such way as we encounter them in everyday life social interactions.

The main methodology employed in most of the experiments of the current PhD work was the visual action adaptation aftereffects paradigm (de la Rosa, Ferstl, et al., 2016; de la Rosa et al., 2014). However, the current PhD work also tried to build on previously existing work and knowledge in the research field of action recognition, and tried to further extend our knowledge to the following questions:

In the first study (Chapter 2: "The Meaning in a Motion: Action Recognition Depends on Semantic Knowledge") we aimed to answer the question **"How are different actions encoded and organized in our brain?"** by comparing the action adaptation aftereffects to different social actions we encounter in everyday life social interactions: handshake, punch, wave and fistbump. Furthermore, we wanted to compare *kinematic* and *semantic* components of action representations, since one line of previous research suggests that distinct kinematic motion patterns of different actions play a crucial role for the encoding of different action representations, while another line of research indicates that the semantic meaning of an action is central for the organization of different action concepts (Ansuini, Cavallo, Bertone, & Becchio, 2014; Prinz, 2014; Pulvermüller, 2005).

In the second study (Chapter 3: "Cross-Cultural Action Recognition: A Comparison Study between Germany vs. Korea") we aimed to answer the question **"Are there cultural differences in action recognition processes?"** by comparing the action adaptation aftereffects to different social actions between German (Western Culture) and Korean (East-Asian Culture) participants. For this, we used the exact same setup and stimuli used in the first study, but extended the tasks to an additional "action naming task" and two "similarity rating tasks". In particular, we were interested in differences in action recognition for the action fistbump, since this action was well-known in Western culture but mostly unknown in Asian cultures. By comparing these two cultures, we wanted to examine the influences of cultural variations on even seemingly basic perceptual processes such as visual recognition of actions (Vogeley & Roepstorff, 2009).

In the third study (Chapter 4: "Visual Adaptation to Actions in Social Interactions: Evidence for Shared Representation of Actions") we aimed to answer the question **"Are representation of actions shared in social interactions?"** by comparing the action adaptation aftereffects to normal and complementary actions in a fully crossed-design consisting of four actions from two pairwise interactions ("Giving-Taking", "Throwing-Catching"). Our predictions were that action adaptation aftereffects should overlap for complementary actions within the same social interaction, if the underlying neural representations are based on shared resources. If not, we should find no overlapping adaptation aftereffects for the complementary actions. Furthermore, we were interested whether there was a difference in the adaptation aftereffects of "initiating" (e.g. Giving or Throwing) or "responding" actions (Taking or Catching). Based on previous research on "Co-Representation" of actions, we expected to find shared representations of actions coupled in a social interaction (Sebanz, Knoblich, & Prinz, 2005; Wenke et al., 2011).

In the fourth and last study (Chapter 5: "The Perception of Cooperativeness without any Visual or Auditory Communication", published in the journal *i-Perception*) we aimed to answer the question **"How do we judge the actions of invisible partners in real interactions?"** by examining the perception of interaction partners after a real-time coupled action-coordination task. Since humans seem to perceive social information of an interaction partner by default, we wondered whether people still do this even without any visual or auditory information about their partner. In a novel experimental setup, we connected two people with a rope and made them accomplish a simultaneously coordinating point-collecting task together while they could not see or hear each other. We wanted to find out whether people still perceive social information – e.g. cooperativeness of an interaction partner – in situations where possibilities for communication are minimal (Engemann, Bzdok, Eickhoff, Vogeley, & Schilbach, 2012; Pfeiffer et al., 2014; Pfeiffer, Timmermans, Bente, Vogeley, & Schilbach, 2011; Rilling & Sanfey, 2011).

1.5. General Discussion and Outlook

The current PhD thesis investigated one of the main questions of social cognition – how we humans understand the actions of other individuals – by examining the perception and recognition of various human social actions in various different contexts. In the following, we briefly summarize all experimental findings and discuss them. We also highlighted methodological novelties used in this PhD work.

1.5.1. Brief Summary of All Experimental Findings

In the first study (Chapter 2), we investigated how different social actions are represented in the brain. We found that differences between action adaptation aftereffects of distinct actions – handshake, punch, wave or fistbump – could be predicted by the perceived kinematic similarities as well as semantic similarities. This implies that action representations are encoded in the brain based on both kinematic motion and the semantic meaning of an action.

In the second study (Chapter 3), we compared processes underlying action recognition between two different cultures – namely Western culture (Germany) and East-Asian culture (Korea). We used an action naming task, similarity rating task, and the same action adaptation aftereffects paradigm as used in the first study. Across all measures, we found little differences in action recognition performances between both cultures, even for an action – fistbump – which was almost completely unknown to the Korean culture. From these results we conclude that action recognition processes are surprisingly robust and consistent across different cultures, at least for Germany and Korea.

In the third study (Chapter 4), we investigated whether there were shared representations of complementary actions involved in social interactions. More concretely, we compared action adaptation aftereffects to actions from two different pairwise interactions – namely Giving & Taking, and Throwing & Catching. Since each action alone was distinct from other actions, by default no one would expect overlapping adaptation aftereffects. However, if the underlying action representations of complementary action pairs are encoded together, one would find overlapping adaptation aftereffects, e.g. between the actions Giving & Taking, or Throwing & Catching. Our results showed that representations of actions in interactions were indeed co-represented; In other words, we found novel evidence for shared representation of actions. Furthermore, we found no differences between "initiating" and "responding" actions for the shared representation of actions. These findings are quite puzzling and call for additional experiments; for example, whether the shared representations are only specific for actions in social interactions, or whether they extend to spatiotemporally contingent and proximal actions (e.g. two different actions which consist of no interaction but were often observed together, for example). On the other hand, these results also allow new insights about how humans can so successfully coordinate their actions together. According to our results, only seeing half of an interaction would be sufficient to be able to react to it. Shared representations of actions may provide an effective anticipatory mechanism for humans to understand others' actions and to engage in more complex social interactions.

In the fourth and last study (Chapter 5), we investigated whether the perception of social information of an interaction partner was possible from blind interaction alone, without any visual or auditory possibilities for communication. Furthermore, we also wanted to find out how the interaction patterns were between physically coupled interaction partners who could not see or hear each other. We found that a reciprocal “turn-taking behavior” emerged in the interactions, and also when expectations for their interaction partners’ “turn-taking behavior” were violated stronger, people more often thought that their partners were male, and bigger in size. These findings imply that people collect social information and make inferences about their interaction partner even when possibilities for communication were minimalistic.

1.5.2. Use of Various Experimental Setups - Including Augmented Virtual Reality

To systematically investigate human social actions, we used cutting-edge motion-capture technologies (MVN Motion Capture Suit from XSense, Netherlands) to record many different real-life social actions and processed them later into brief dynamic movie stimuli. We showed these recorded actions as standard point-light-stimuli (Chapter 2 and 3), as well as mapped on a life-sized 3D human avatar using augmented, immersive virtual reality (Chapter 4).We used this novel augmented reality setup where a life-size three-dimensional female avatar was facing participants in order to mimic realistic social interactions. Since real life interactions are normally subject to greater variations and noise, this novel 3D-augmented reality setup enabled us measures in a more controlled experimental environment while still providing a convincing perception of realistic social interaction to the participants.

1.5.3. Use of Robust, Reliable Task Measures

To examine the underlying representations of specific visual processes, we repeatedly used a visual action adaptation aftereffect paradigm, initially developed by Dr. Stephan de la Rosa (de la Rosa, Ekramnia, et al., 2016; de la Rosa, Ferstl, et al., 2016; de la Rosa et al., 2014). The adaptation aftereffect paradigm enabled us to more reliably and more specifically study the underlying action representations of various different human social actions. Using the adaptation paradigm, we examined differences between several social action representations in terms of their similarities in kinematic motion and semantic meaning (Chapter 2), differences in action recognition processes across distinct cultures such as Germany and Korea (Chapter 3), and tested shared representations underlying complementary actions in dyadic interactions (Chapter 4).

1.5.4. Advances Towards More Innovative Measures in Social Interactions

To examine the dynamics of real-time social interaction between different individuals, we developed a novel coordination task where two humans were physically connected with a climbing rope wearing a harness, but could not see or hear each other. Participants had to accomplish a point-collecting task together while being connected to each other, and coordinate movements without visual or auditory communication (Chapter 5). We examined the coordination behavior of participants as well as their social perception and judgments of their interaction partners in this unusual situation. With this novel task, we found out that a reciprocal "turn-taking behavior" naturally emerged in the initial interactions between participants, and that people collected and made social inferences about their interaction partner although possibilities for communication and social information exchange were minimal. In order to truly understand how humans process various kinds of social information about each other, we need more innovative experimental measures involving real-time social interaction.

In summary, the current PhD thesis attempts to advance our knowledge about how we understand other humans, and the current work provides new insights into the brain mechanisms how humans understand other people through the perception and recognition of social actions inside and outside of social interactions.

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Declaration of the Contribution of the Candidate

This thesis comprises of four manuscripts that were, at the time of the thesis submission, either accepted or submitted for publication. The ideas for the studies have been all proposed by the candidate. The bibliographic details of the studies and where they appear in the thesis are set out below, together with a description of the contribution of each author.

Study 1 (Chapter 2):

Chang, D-S., Giese, M.A., Vogeley, K., Wong, H.Y., Bülthoff, H.H., & de la Rosa, S. (2016). The Meaning in a Motion. Action Recognition Depends On Semantic Knowledge. (under review) The idea for this study was proposed by the candidate. The experimental design and implementation was predominantly developed by the candidate based on existing previous experimental work of S.R. Data collection and analysis, and writing of the manuscript was performed by the candidate. S.R. helped with supervision, development of the experimental design, recording and processing the stimuli, and data analysis. S.R. and H.H.B. provided the technical setup for performing the experiments. S.R., M.A.G., K.V., H.Y.W. and H.H.B. helped with their expertise, knowledge and critical comments for the interpretation of data and revision of the manuscript.

Study 2 (Chapter 3):

Chang, D-S., Kim, J-S., Ju, U-J., Wallraven, C., Bülthoff, H.H., & de la Rosa, S. (2016). A Cross-Cultural Comparison Study of Social Action Recognition in Germany vs. Korea.(under review) The idea for this study was proposed by the candidate. The experimental design and implementation was predominantly developed by the candidate based on existing previous experimental work of S.R. Data collection in Korea was performed by K.J. and J.U, with the help of C.W, and data collection and analysis, writing of the manuscript was performed by the candidate. S.R. helped with supervision, stimuli, and data analysis. S.R. and H.H.B. provided the technical setup for performing the experiments. S.R., C.W. and H.H.B. helped with their expertise, knowledge and critical comments for the interpretation of data.

Study 3 (Chapter 4):

Chang, D-S.[*], Fedorov, L.[*], Giese, M.A., Bülthoff, H.H., & de la Rosa, S[*]. (2016). Visual Adaptation to Actions in Social Interactions: Evidence for Shared Representation of Actions. [*These authors contributed equally to the experiment] (under review) The idea for this study was proposed by the candidate. The experimental design and implementation was developed by the candidate, together with L.F. and S.R. Data collection and analysis was also performed together with L.F. and S.R. Writing of the manuscript was performed by the candidate. The supervision of the experiment with their expertise, knowledge and critical comments was done by S.R., M.A.G. The technical setup for performing the experiments was provided by S.R. and H.H.B.

Study 4 (Chapter 5):

Chang, D-S., Burger, F., Bülthoff, H.H. & de la Rosa, S. (2015). The Perception Of Cooperativeness Without Any Visual Or Auditory Communication. (Published in the Open-Access-Journal *i-Perception*, doi:10.1177/2041669515613671.) The idea for this study was proposed by the candidate. The experimental design and implementation was developed by the candidate, data collection and analysis was also performed by the candidate. F.B. helped with data collection and setup of experimental design. S.R. helped with supervision, further development of ideas for the experimental design, and data analysis. The candidate wrote the manuscript, and S.R. and H.H.B. helped with revision of the manuscript.

Parts of this PhD work have been also presented at the following conferences & symposia and workshops, with some of the work published as conference proceedings:

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (August-2013): Making Trait Judgments based on Biological Motion Cues: A Thinslicing Approach. ACM Symposium on Applied Perception (SAP '13), Dublin, Ireland.

- Chang D-S. (September-2013) Perception of Social Cues and Prediction of Cooperation in the Brain. Networks! 2013: 4th German Neurophysiology PhD Meeting, Tübingen, Germany.

- Chang D-S., & de la Rosa, S. (March-2014) Beyond Action Recognition: Making Social Inferences from Action Observation. Interdisciplinary College Spring School 2014: Cognition 3.0 - the social mind in the connected world, Günne, Germany.

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (May-2014): Visual Adaptation to Social Actions: The Role of Meaning vs. Motion for Action Recognition. 79th Cold Spring Harbor Symposium on Quantitative Biology: Cognition, New York, NY, USA.

- Chang D-S., Bülthoff H.H. & de la Rosa, S. (June-2014): Visual Adaptation to Social Actions: The Role of Meaning vs. Motion for Action Recognition, 6th International Conference on Brain and Cognitive Engineering (BCE 2014), Tübingen, Germany.

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (August-2014): Does Action Recognition Depend more on the Meaning or Motion of Different Actions? 37th European Conference on Visual Perception (ECVP 2014), Beograd, Serbia, Perception, 43(ECVP Abstract Supplement) 103.

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (September-2014): Actions revealing cooperation: predicting cooperativeness in social dilemmas from the observation of everyday actions. 12th Biannual Conference of the German Cognitive Science Society (KogWis 2014), Tübingen, Germany, Cognitive Processing, 15(Supplement 1) S33-S34.

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (September-2014) Action recognition and the semantic meaning of actions: how does the brain categorize different social actions? 12th Biannual Conference of the German Cognitive Science Society (KogWis 2014), Tübingen, Germany, Cognitive Processing, 15(Supplement 1) S95.

- Chang D-S., Ju U, Bülthoff H.H., & de la Rosa, S. (September-2015): How different is Action Recognition across Cultures? Visual Adaptation to Social Actions in Germany vs. Korea. 15th Annual Meeting of the Vision Sciences Society (VSS 2015), St. Pete Beach, FL, USA, Journal of Vision, 15(12) 493.

- Chang D-S., Burger F, Bülthoff H.H., & de la Rosa, S. (March-2015) Differences in Behavior and Judgments during interaction with a rope without seeing or hearing the partner. Symposium on Reciprocity and Social Cognition, Berlin, Germany.

- Chang D-S., & de la Rosa, S. (May-21-2015) Action Recognition & Social Interaction: New Experimental Paradigms, Rutgers University, Center for Cognitive Science, New Brunswick, NJ, USA.

- Chang D-S., Bülthoff H.H., & de la Rosa, S. (July-2015) Action Recognition Across Cultures? Symposium on Diversity of Social Cognition, Köln, Germany.

Geschrieben steht: »Im Anfang war das Wort!«

Hier stock ich schon! Wer hilft mir weiter fort?

Ich kann das Wort so hoch unmöglich schätzen,

Ich muß es anders übersetzen,

Wenn ich vom Geiste recht erleuchtet bin.

Geschrieben steht: Im Anfang war der Sinn.

Bedenke wohl die erste Zeile,

Daß deine Feder sich nicht übereile!

Ist es der Sinn, der alles wirkt und schafft?

Es sollte stehn: Im Anfang war die Kraft!

Doch, auch indem ich dieses niederschreibe,

Schon warnt mich was, daß ich dabei nicht bleibe.

Mir hilft der Geist! Auf einmal seh ich Rat

Und schreibe getrost: **Im Anfang war die Tat!**

- Johann Wolfgang von Goethe, Faust, 1808

It says: “In the beginning was the Word.”

Already I am stopped. It seems absurd.

The Word does not deserve the highest prize,

I must translate it otherwise

If I am well inspired and not blind.

It says: In the beginning was the Mind.

Ponder that first line, wait and see,

Lest you should write too hastily.

Is Mind the all-creating source?

It ought to say: In the beginning there was Force.

Yet something warns me as I grasp the pen,

That my translation must be changed again.

The spirit helps me. Now it is exact.

I write: **In the beginning was the Act.**

- Johann Wolfgang von Goethe, Faust, 1808

2 The Meaning in a Motion: Action Recognition Depends on Semantic Knowledge

The current chapter has been reproduced from the draft of an article that was submitted for publication: "The Meaning in a Motion: Action recognition depends on semantic knowledge" by Dong-Seon Chang, Martin A. Giese, Kai Vogeley, Hong Yu Wong, Heinrich H. Bülthoff and Stephan de la Rosa, submitted and currently under review.

2.1. Abstract

Action recognition is crucial for humans since the ability to recognize different actions fast and accurately is indispensable for successful human social interaction. One of the central questions in action recognition concerns the organization principles of action representations. Previous research suggests that distinct kinematic motion patterns of different actions play a crucial role for the encoding of different action representations, while other research indicates that the semantic meaning of an action is central for the organization of different action concepts. However, it is unclear whether and how these two different approaches are related to each other. Here, we aimed to combine these two different approaches on action recognition using an action adaptation aftereffect paradigm. We conducted two experiments to examine the role of kinematic motion patterns or semantic meanings for action representations. In the first experiment, participants judged the similarity between different actions either based on motion kinematics or the semantic meaning of an action. These judgments were then used to predict the adaptation aftereffects of the different actions. In the second experiment, we compared the adaptation aftereffects of original actions with computer-generated morphs of kinematically distorted actions which either retained semantic meanings (i.e. exaggerated action) or not (i.e. nonsense action). In both experiments, analysis of the action adaptation aftereffects showed a significant influence of semantic meaning for the recognition of different actions. These results imply that not only perceived kinematic differences but also previously learned semantic knowledge about the meaning of an action plays an important role for the organization of action representations.

Keywords: Action recognition; Adaptation; Aftereffects; Biological Motion; Categorization

2.2. Introduction

In everyday life, we encounter numerous sorts of actions carried out by different people. Imagine a stranger suddenly approaching and stretching out his fist. Our brain has to decide within less than a second whether this action is going to be dangerous (e.g. a punch) or friendly (e.g. a fist bump), potentially with immediate consequences. Research in the past has shown that humans are excellent at recognizing actions (Blake & Shiffrar, 2007; Giese, 2015). Humans can almost instantaneously categorize different sorts of movements such as walking, running, dancing or boxing even from visually impoverished motion stimuli (Dittrich, 1993; Johansson, 1973; van Boxtel & Lu, 2011), and we can also readily distinguish whether actions are performed by familiar people such as friends or strangers (Cutting & Kozlowski, 1977; Loula, Prasad, Harber, & Shiffrar, 2005b; Prasad & Shiffrar, 2009). Moreover, people can infer the intentions and goals of different actions why they are performed (Ansuini et al., 2014; Becchio, Manera, Sartori, Cavallo, & Castiello, 2012; Becchio, Sartori, Bulgheroni, & Castiello, 2008b; Becchio, Sartori, & Castiello, 2010). All these findings imply the importance of action representations in the brain, although the underlying organization principle for the representations of different actions has remained a matter of debate (Buccino et al., 2001; Buxbaum & Kalénine, 2010; Giese & Rizzolatti, 2015; Grafton & Hamilton, 2007; Huth, Nishimoto, Vu, & Gallant, 2012; Jeannerod, 1994, 1999, 2006; Lingnau & Downing, 2015; Prinz, 2014; Watson, Cardillo, Ianni, & Chatterjee, 2013; Wiggett & Downing, 2011).

Previous studies on action recognition have highlighted the relevance of low-level visual cues and kinematic information in action representations. A substantial amount of research had been devoted to various spatiotemporal and neurophysiological aspects of visual action recognition (Casile et al., 2010; Georgescu et al., 2014; M. Giese, Thornton, & Edelman, 2008; Jellema & Perrett, 2006; Ortigue, Thompson, Parasuraman, & Grafton, 2009;

Puce & Perrett, 2003; Theusner et al., 2014; Vangeneugden, Pollick, & Vogels, 2009). Based on physiological findings, several computational models had also been suggested how complex physical movement patterns can be explained by visual pathways covering local motion or form cues (Giese & Poggio, 2003; Lange & Lappe, 2006) or how physical properties of body motion patterns could be encoded in perceptual spaces (Giese et al., 2008; Thurman, Giese, & Grossman, 2010). Recent studies have further tried to explain how humans perceive the intentions of other people and infer these from the movement kinematics of performed actions (Ansuini et al., 2014; Becchio et al., 2014; Becchio, Sartori, Bulgheroni, & Castiello, 2008a; Becchio et al., 2010; J. Kilner, Friston, & Frith, 2007; Sartori, Becchio, & Castiello, 2011). However, many of these studies approached action recognition mostly focusing on non-conceptual, sensorimotor aspects of action representations (e.g. movement kinematics).

In contrast, and unrelated to the literature mentioned above, other studies have started to focus on conceptual, semantic aspects of action knowledge linking the movements of actions with the underlying concepts corresponding to these actions (Buxbaum & Kalénine, 2010; Gallese & Lakoff, 2005; Glenberg & Gallese, 2012; Kiefer & Pulvermüller, 2012; Prinz, 2014; Pulvermüller, 2005; Watson et al., 2013). Evidence for this link is drawn from lesion studies and aphasia patients (Saygin, Wilson, Dronkers, & Bates, 2004; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003), action-sentence-compatibility effects (Glenberg & Gallese, 2012; Glenberg & Kaschak, 2002; Taylor, Lev-Ari, & Zwaan, 2008; Zwaan & Taylor, 2006), studies with action prediction or production paradigms (Liepelt, Dolk, & Prinz, 2012; Springer, Huttenlocher, & Prinz, 2012; Springer & Prinz, 2010), and neuroimaging studies showing overlapping brain areas during the performance of actions and the reading of action-related words (Aziz-Zadeh & Damasio, 2008; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermüller, 2004; Pulvermüller, 2005). These studies suggest that similar brain mechanisms are involved in the processing of both language and actions. This might be taken to suggest that semantic knowledge plays an important role in understanding the meaning of an action. However, the main experimental methodologies used in the studies examining semantic knowledge and action concepts differ considerably from the action recognition studies focusing on low-level kinematic visual cues, making direct comparisons between these two different approaches rather difficult (Prinz, 2014).

Only recently research has started to examine how visual information about different movement kinematics is linked to semantic knowledge of action concepts. Recent research examining the interplay of low-level visual action information and high-level action concepts has found that visually identical actions can be associated with multiple action interpretations (de la Rosa et al., 2015), and that action representations are sensitive to the semantic context in which an action is embedded (de la Rosa, Streuber, Giese, Bülthoff, & Curio, 2014). However, these studies have mainly used static snapshot stimuli of actions, leaving out explicit links to dynamic movement kinematics. Thus, no studies have directly compared the influence of both movement kinematics and semantic knowledge in action representations yet.

In the present study, we wanted to investigate whether representations of different social actions are more sensitive to kinematic features of an action or to the semantic content encoded in an action. We targeted action-specific representations by means of an action adaptation aftereffect paradigm (de la Rosa et al., 2014). Adaptation aftereffect paradigms have widely been used to examine specific visual recognition processes in the human brain both with low-level visual processes such as color, motion or orientation, and with more complex visual stimuli such as face, gender or social actions (Armann, Jeffery, Calder, & Rhodes, 2011; Barraclough & Jellema, 2011; Clifford et al., 2007; Clifford & Rhodes, 2005; de la Rosa et al., 2014; Jordan, Fallah, & Stoner, 2006; Keefe, Dzhelyova, Perrett, & Barraclough, 2013; Leopold, O'Toole, Vetter, & Blanz, 2001; Troje, Sadr, Geyer, & Nakayama, 2006; Webster & MacLeod, 2011). In an adaptation aftereffect paradigm, participants view the same stimulus (e.g. a red color) for a prolonged time, and report the perception of a subsequently presented neutral or ambiguous test stimulus (e.g. the color white). It is typically found that the perception of the test stimulus is systematically altered leading to an antagonistic shift in perception (e.g. seeing the color green). This aftereffect is explained by decreased firing of the underlying neuronal units specifically responding to the repeatedly shown stimulus, resulting in a measurable response change of visual processes due to the prolonged exposure to the adaptor stimulus. The response change affects the perception of the following test stimulus, given that both the adaptor and test stimulus share at least partly the same underlying visual processes. Thus, by examining the adaptation aftereffect of different adaptors on the same test stimulus, one can measure whether and how much these stimuli share the same putative underlying neural representations. For instance, previous studies have succeeded to examine the neural representations of different face identities in the brain using distinct high-level adaptation aftereffects for different face morphs, further demonstrating that adaptation aftereffect paradigms provide an elegant way to examine high-level visual representations (Clifford & Rhodes, 2005; de la Rosa, Streuber, Giese, Bülthoff, & Curio, 2013; Jiang, Blanz, & O'Toole, 2006; Leopold et al., 2001; Rhodes et al., 2007).

We conducted two experiments in which we used the action adaptation aftereffect paradigm to assess the underlying action representations of different social actions. In the first experiment, we reasoned that if motion kinematics and semantic meanings of an action are crucial for modulating the action representations, the size of the action adaptation aftereffects should correlate with the ratings of perceived motion kinematics and semantic meanings of an action. Following this logic, in Experiment 1 we examined the degree to which the perceived differences in motion kinematics or semantic meanings of an action predicted the action adaptation aftereffects for different social actions. In the second experiment, we wanted to further investigate whether the recognized semantic meaning of an action was necessary for the emergence of action adaptation aftereffects. For this, we created novel action stimuli by distorting the motion kinematics of two actions in identical ways, but making the perceived semantic meanings of those actions differ from each other: one action appearing like a "caricature" (with semantic meaning) and the other action appearing like "nonsense" (without semantic meaning). We examined whether the distortion of the motion kinematics by itself or the differently perceived semantic meanings of the actions influenced the measured action adaptation aftereffects.

2.3. Experiment 1: Comparing Motion vs. Meaning of Different Actions

In Experiment 1, we examined the degree to which the kinematic or semantic information influenced the action adaptation aftereffects. Participants viewed four different social actions – handshake, punch, wave, fistbump – pairwise and were asked to rate perceived differences between two actions in terms of their motion kinematics or semantic meanings. Subsequently, participants took part in a psychophysical adaptation experiment where each social action was shown as an adaptor. We calculated the pairwise differences in the adaptation aftereffects between each condition and used the ratings of the motion kinematics and semantic meanings to predict these differences in action adaptation aftereffects.

The test stimuli in the adaptation experiment always consisted of ambiguous action stimuli morphed between the actions handshake and punch. The social actions were chosen in such way because handshake and punch were expected to be maximally different in terms of both motion kinematics and semantic meanings, whereas the other two actions were expected to be distinctly different from handshake or punch either with respect to the motion kinematics or to the semantic meanings. For example, we expected the action fistbump to be rated similar to punch in terms of motion kinematics, but similar to handshake in terms of semantic meanings.

The logic of this experimental design was as follows: If two actions share underlying representations they will show similar action adaptation aftereffects even with different adaptors, whereas if they do not share any common processes no action adaptation aftereffects are expected for different adaptors. By predicting the size of these measured action adaptation aftereffects for different social actions from either the kinematic or semantic similarity ratings, we wanted to find out whether the representations of actions were more related to the kinematic or semantic information coded in the actions.

2.3.1. Methods

2.3.1.1. Participants

We recruited 24 participants (mean age=29.34 ± 7.08 years, female=15, male=9) for Experiment 1 using the Tuebingen MPI subject database. All participants were appropriately informed about the experiment and signed an informed consent. All participants had normal vision and hearing. They were all naïve concerning the hypotheses of the experiment. The experiment was conducted in line with the Declaration of Helsinki and in accordance with the recommendations of the ethics board of the University of Tuebingen.

2.3.1.2. Stimuli and Apparatus

We used an inertia-based motion capture suit (MOVEN Motion Capture Suit from XSense, Netherlands) to record different social actions. We chose four different social actions: handshake, wave, punch and fist bump. All actions were recorded from one person starting from a neutral pose, and lasted approximately 1.5 seconds in average to be fully carried out. All actions were cut and processed into standardized short movies of point-light-dots (Johansson, 1973) stimuli (number of frames = 160, refresh rate = 120 frames per second (fps)), showing only the joint movements (number of joints shown in the movie = 15) of an actor. All actions were presented from the side view. Each of the recorded social actions was used as adaptor stimuli in the adaptation aftereffect experiments, whereas the test stimuli were action morphs between two different actions (i.e. handshake and punch). Action morphs were generated by taking the weighted average linear distance between the joint positions in space for each recorded frame of an action. We used eight different morph weights between two actions ranging from 0% of action 1 until 100% of action 2 (morph weights: 0, 0.3, 0.6, 0.67, 0.73, 0.8, 0.9, 1). Morph weights were determined in pilot trials where we found that most participants' point of subjective equality (PSE) for the stimuli were between the morph weights 0.6 and 0.8. Each morphed action was shown 18 times in each adaptor condition with the presentation order being completely randomized. All stimuli were presented on a LCD monitor (refresh rate of 60 Hz; screen resolution of 1280 x 1024 pixels) using MATLAB and the Psychophysics Toolbox.

2.3.1.3. Procedure

First, all participants were instructed about the general purpose of the experiment and informed about the four different social actions – handshake, punch, wave, fist bump – used in Experiment 1. Participants rated all possible pairs of the four social actions in terms of their perceived differences in either semantic meaning or kinematic motion on a visual analogue scale ranging from 0 (exactly same) to 10 (completely different) to quantify the perceived differences between the actions in terms of their meaning or motion. The adaptation experiment consisted of five experimental blocks, always starting with a block of trials where participants watched all test stimuli without the presentation of an adaptor in order to measure participants' perception of the test stimuli without adaptation (baseline). The following four experimental blocks of trials each probed a different adaptor (handshake, punch, wave, fist bump), and the order of these blocks were completely balanced across all participants. Each experimental block consisted of a total 144 trials (8 different morph levels x 18 randomized repetitions of test stimuli). Each block started with an initial adaptation phase consisting of 30 presentations of the adaptor stimulus (inter-stimulus-interval (ISI) = 200 milliseconds), then experimental trials began. On each trial, three repeated presentations of one adaptor stimulus were followed by a test stimulus presented on a screen and participants had to judge which action they recognized (e.g. “Did you see a handshake or a punch?”) in a 2-alternative-forced-choice (2AFC) task. The ISI between the adaptor stimuli and test stimuli were 100 milliseconds, and a beep tone always preceded the presentation of the test stimuli. The next trial started as soon as the participants gave the answer by pressing a button on the keyboard. In short, the test stimuli were presented according to the psychophysical method of constant stimuli. The total number of trials for each participant was 720 trials (5 experimental blocks x 8 different morph levels x 18 randomized repetitions of test stimuli). Participants took approximately 2 hours to finish the whole experiment, including 5-10 minutes breaks between each experimental block. After the whole experiment, the participants filled out a feedback questionnaire with general questions about the experiment.

2.3.1.4. Analysis of Data

We calculated the action adaptation aftereffects for each action by fitting psychometric functions to the data describing the proportion of ‘punch’ responses in each adaptor block as a function of the morph levels of the test stimuli. We used a Weibull function with α (position of the psychometric function along on the x-axis) and β (slope of the psychometric function), and γ (lapse rate) as free parameters (gamma was fixed to 0), following the same analysis procedure as in our previous study (de la Rosa et al., 2014). Using the psychometric function we determined the point of subjective equality (PSE) – i.e. the morph level for which participants gave an equal amount of ‘punch’ and ‘handshake’ answers – for each adaptor condition and participant separately. The adaptation aftereffect was defined as the shift of perceptual change in each adaptor block – difference in PSE values between the adaptor and baseline conditions – for the same test stimuli.

2.3.2. Results and Discussion

The mean ratings of semantic meaning and kinematic motion were summarized using multidimensional scaling (MDS). The MDS revealed distinct patterns for the perceived differences in terms of kinematic motion and semantic meaning. As expected, punch and fistbump were rated more similar to each other in terms of the kinematic motion but not in terms of semantic meaning. Fistbump and handshake were rated more similar to each other in terms of semantic meaning but not in terms of kinematic motion. Punch and handshake were rated to be different from each other both in terms of semantic meaning and kinematic motion. Wave was rated neither very similar nor very different in both semantics and kinematics (Figure 2-1A and 2-1B).

The action adaptation effects for each action are shown and summarized in Figure 2-1C. We used these individual action adaptation aftereffects for each action to calculate all pairwise differences of PSE values between the different adaptor conditions (Figure 2-1D). These differences in adaptation aftereffects were then predicted by the previously obtained ratings of differences in kinematic motion and semantic meaning using an additive linear mixed model (Baayen, Davidson, & Bates, 2008; Barr, Levy, Scheepers, & Tily, 2013). We used participants as a random factor and the ratings of kinematic motion and semantic meaning as fixed factors. Intercepts were allowed to be random for each participant.

Both kinematic motion ($\chi^2 (1) = 15.03$, $p < 0.001$) and semantic meaning ($\chi2 (1) = 8.96$, $p < 0.01$) significantly predicted the adaptation aftereffects for the different actions. These results of Experiment 1 imply that representations of different social actions seem to be encoded and organized in terms of kinematic motion as well as semantic meaning in the brain.

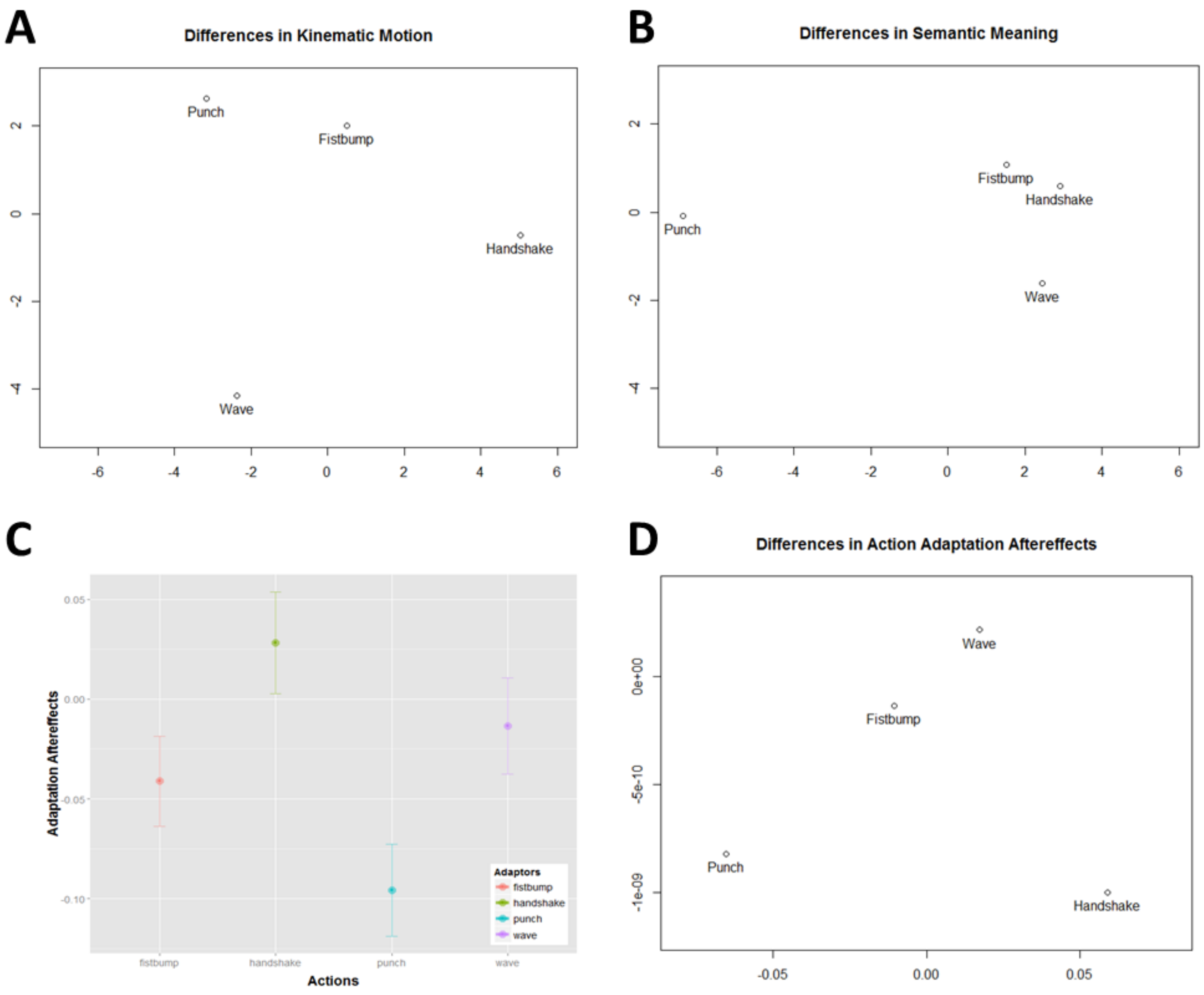

Figure 2-1. Measured differences between social actions. A: Differences between the adaptor stimuli in terms of semantic meaning fitted with a MDS. **B:** Differences between the adaptor stimuli in terms of kinematic motion fitted with a MDS. For both A and B, larger distances in the plot indicate larger perceived differences, and the distances between the points indicate the mean rating of all participants. **C:** Mean action adaptation aftereffects are shown for each adaptor condition separately on the x-axis, and the values on the y-axis indicate the shift of the PSE from baseline condition in the measured psychometric curves for each action. Error bars indicate the standard error of the mean. **D:** All pairwise mean differences between action adaptation effects of the actions in C have been summarized on a two-dimensional scale with a MDS for the purpose of illustration. The distances between the actions indicate differences between the action adaptation aftereffects for each action.

2.4. Experiment 2: The Role of Semantic Meaning for Action Recognition

In Experiment 1, we found that both kinematic and semantic information had an influence on the measured action adaptation aftereffects. In Experiment 2, we wanted to focus more on semantic action information and test for the possibility that semantic knowledge of actions – correctly recognizing the meaning of an action – was a necessary constituent for the representation of actions. To test this, we created two novel actions by distorting the kinematic information of two original actions – a push and a hug – in identical ways, but with different degrees of recognizable semantic meanings in the actions, so that the action push was perceived as exaggerated (“caricature”), and the action hug not recognized as a meaningful action at all (“nonsense”). We measured the action adaptation aftereffects of all four actions and compared the action adaptation aftereffects with each other.

The logic of the experiment was as follows: We compared the action adaptation aftereffects of the distorted actions with the undistorted actions. If kinematic information mattered predominantly for action representations, then the adaptation aftereffects of the distorted novel actions should equally diminish, since the degree of distortion for the action kinematics was equal (i.e. same morph algorithm and morph level) for both novel actions. However, if semantic knowledge of actions was crucial for action representations, the adaptation aftereffects of the distorted novel actions should depend on whether the meaning of an action was recognizable or not. In this case, the adaptation aftereffect of the “caricature” action should be more similar to the undistorted original action, whereas the “nonsense” action should show a strongly diminished action adaptation aftereffect and be significantly different from the undistorted original action.

2.4.1. Methods

2.4.1.1. Participants

We recruited 18 participants (mean age= 26.67 ± 7.76 years, female=12, male=6) for Experiment 2 using the Tuebingen MPI subject database. All participants were appropriately informed about the experiment and signed an informed consent. All participants had normal vision and hearing. They were all naïve concerning the hypotheses of the experiment. The experiment was conducted in line with the Declaration of Helsinki and in accordance with the recommendations of the ethics board of the University of Tuebingen.

2.4.1.2. Stimuli and Apparatus

The adaptor stimuli were four different actions whereas two actions – push, hug – were originally recorded with the same setup as in Experiment 1, and two novel actions (“caricature”, “nonsense”) were created by morphing and distorting the motion parameters of the two original actions. To generate novel actions, we used the same morph algorithm for the generation of the action morphs in Experiment 1 and created novel actions by extrapolating the actions in morphing space to 200% of the original actions (i.e. distances between each joint, as well as the movements of each joint point were doubled). The resulting novel actions were strongly distorted and appeared clearly impossible for humans to perform. This was confirmed by questionnaires where all participants agreed that the novel actions looked impossible for a human to perform and did not look like normal human actions. When asked to freely categorize the actions, all participants answered that the 200%-over-morphed-push (= “caricature” action) looked like a “really exaggerated push” or a “really strong push”, but were unable to name which action the 200%-over-morphed-hug was (= “nonsense” action). All actions (push, hug, “caricature”, “nonsense”) were cut and processed into standardized short movies of point-light-dots stimuli (number of frames = 167, refresh rate = 120 fps), and presented from the side view showing the same number of joint movements (n=15) as in Experiment 1. The adaptor stimuli were shown in exactly same way as in Experiment 1 (e.g. same repetition number, ISI). The test stimuli always consisted of morphs between the actions push and hug, which were presented in seven different morph steps (0, 0.175, 0.35, 0.4, 0.6, 0.8, 1) in a completely randomized order. When the test stimulus was presented on the screen participants had to judge which action they recognized (e.g. "Did you see a push or a hug?") in a 2AFC task. Otherwise, all conditions (number of adaptor repetitions, test stimuli repetitions, ISI) including the design, setup, apparatus and procedure used was kept identical as in Experiment 1.

2.4.1.3. Procedure

Experiment 2 followed the exact same procedure as in Experiment 1, consisting of one baseline block of trials at the beginning and four experimental blocks of trials consisting of the same adaptor stimuli ("push", "hug", "caricature", "nonsense"). The order of experimental blocks for the different actions was balanced across participants.

2.4.1.4. Analysis of Data

We calculated the action adaptation aftereffects for each action by fitting psychometric functions to the data describing the proportion of 'push' responses in each adaptor block as a function of the morph levels of the test stimuli. We used the same Weibull function with α (position of the psychometric function along on the x-axis) and β (slope of the psychometric function), and γ (lapse rate) as free parameters (gamma was fixed to 0) as in Experiment 1. Using the psychometric function we determined the point of subjective equality (PSE) – i.e. the morph level for which participants gave an equal amount of 'push' and 'hug' answers – for each adaptor condition and participant separately. The adaptation aftereffect was defined as the shift of perceptual change in each adaptor block – difference in PSE values between the adaptor and baseline conditions – for the same test stimuli across all participants. Otherwise, all analysis of data followed the same analysis procedure as in Experiment 1.

2.4.2. Results and Discussion

A one-way within subjects analysis of variance revealed a significant main effect for adaptor actions ($F(1,17) = 99.97$, $p < 0.001$), and a significant interaction between adaptor actions and kinematical distortion ($F(1,17) = 5.06$, $p = 0.038$). Post hoc comparisons with paired samples *t*-tests showed that action adaptation aftereffects for the two original undistorted actions were both significantly different from the baseline condition (action push: $t(17) = -2.29$, $p = 0.035$, action hug: $t(17) = 4.09$, $p < 0.001$). The action adaptation aftereffects for the two novel distorted actions showed different patterns compared to each other and the original actions (see Figure 2-2). The adaptation aftereffect for the "caricature" action – originally derived from the action push and semantically categorized as an exaggerated push – was also significantly different from the baseline condition ($t(17) = -2.13$, $p = 0.047$), and significantly correlated with the adaptation aftereffect of the original action push ($r(16) = 0.69$, $p = 0.001$). The adaptation of the "nonsense" action – originally derived from the action hug, but not meaningfully categorized at all – did not significantly differ from the baseline condition ($t(17) = 0.68$, $p = 0.504$), and was also significantly different from the original action hug ($t(17) = 2.75$, $p = 0.014$). In brief, the "caricature" action showed a similar adaptation aftereffect compared with the original action ("push"), whereas the "nonsense" action resulted in a strongly diminished adaptation aftereffect (similar to the baseline condition) and a significantly different adaptation aftereffect compared with the original action ("hug").

These findings are consistent with our initial predictions, and point out that action recognition depends on the semantic knowledge of actions. The adaptation aftereffects only diminished for the distorted action where the semantic categorization of meaning was impossible, although both novel actions were equally distorted in terms of motion kinematics. Thus it seems that correctly recognizing the meaning of an action plays a crucial role for the modulation of the underlying action representations.

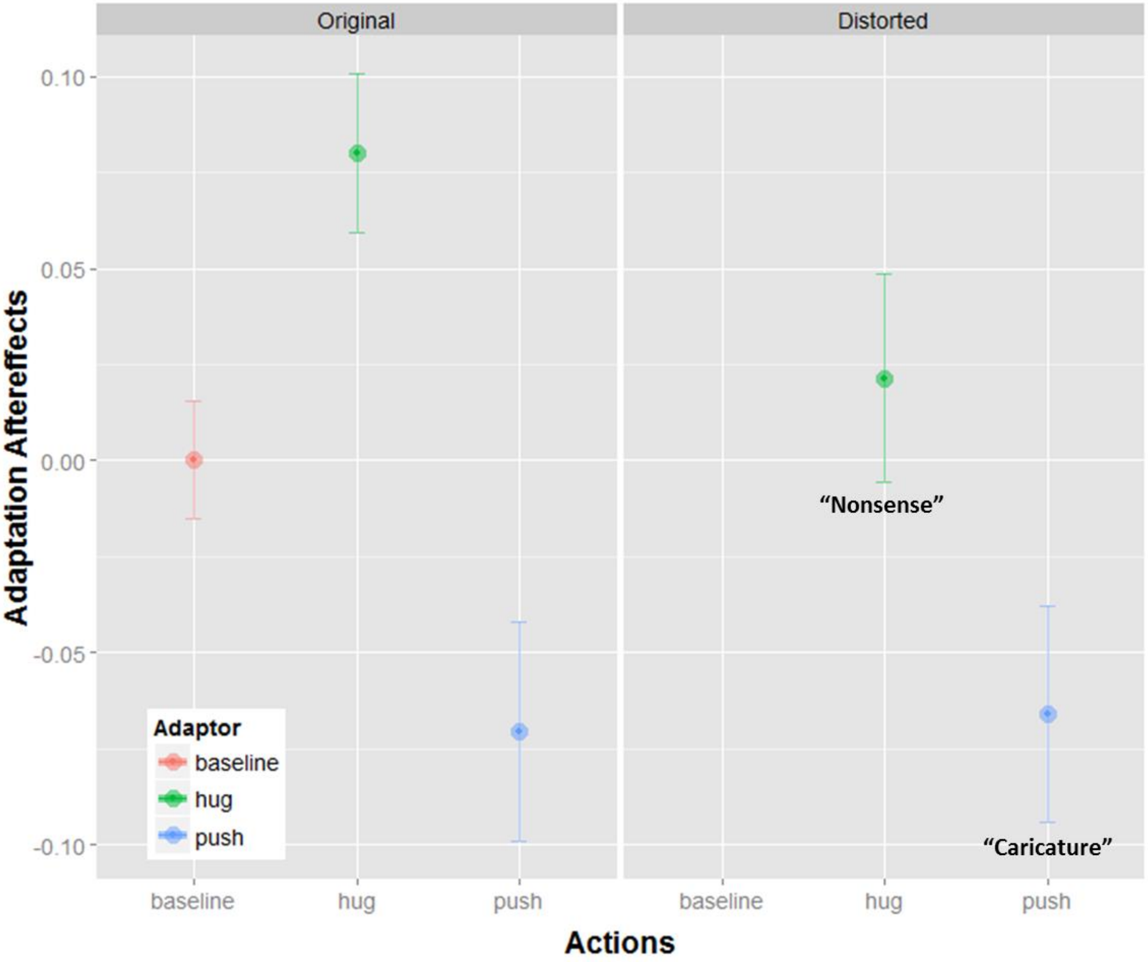

Figure 2-2. Comparing adaptation aftereffects for all actions used in Experiment 2. Adaptation aftereffects are shown for baseline (no adaptor) and each adaptor conditions: two original, undistorted actions (hug, push) and two novel, kinematically distorted actions (distorted push = "caricature", distorted hug = "nonsense"). Action adaptation aftereffects were measured from the different PSE (Point of Subjective Equality) values of the psychometric curve measured for each action in all participants. The x-axis depicts the different adaptors, and the values on the y-axis indicate the shift of the PSE from baseline condition in the measured psychometric curves for each action. Each point for an action is the average of all 18 participants, and error bars indicate the standard error of the mean.

2.5. General Discussion

The main aim of the present study was to investigate whether representations of different social actions are more sensitive to kinematic features of an action or to the semantic content encoded in an action. It has been previously noted that there is a strong divide between research focusing on non-conceptual and procedural aspects (e.g. low-level motion cues, movement kinematics) or conceptual semantic aspects (e.g. specifying the meaning of an action, language comprehension studies) of action representations (Prinz, 2014). Our study provides first results aiming to combine these two different approaches by directly comparing kinematic vs. semantic influences on action representations using an action adaptation aftereffect paradigm. The experiments reported here confirm that both kinematic and semantic information play an important role for the organization of action representations, and further show that semantic knowledge of actions plays a crucial role for action recognition.

2.5.1. Organization of action representations: Action maps in the brain?

Humans are able to recognize thousands of distinct actions from different persons in various contexts and environments (Huth et al., 2012; Klatzky, Pellegrino, McCloskey, & Lederman, 1993; Watson & Buxbaum, 2014). How does the brain effectively represent information about these different actions? What would be an efficient organization principle for the representation of actions?

Organizing actions by their movement components and kinematic similarities is one obvious candidate for a criterion to organize actions. It had been suggested that similarities between the movement kinematics of actions can be determined by the firing patterns of visual temporal cortical neurons in macacque monkeys using a parametric action space (Vangeneugden et al., 2009). Studies in macacque monkeys have also shown that electrical stimulation of the motor cortex can invoke specific movements of the arm targeting a fixed location in space, whereas stimulation of adjacent neurons would target similar areas in space, so that it produces similar movements (Cooke, Taylor, Moore, & Graziano, 2003; Graziano, Taylor, & Moore, 2002; Graziano, Aflalo, & Cooke, 2005). These findings have been replicated in rodents (Brecht, Schneider, Sakmann, & Margrie, 2004; Cramer & Keller, 2006; Ramanathan, Conner, & Tuszynski, 2006), and a generalized and extended account based on these findings suggests that a map of behaviorally relevant complex actions exists in the motor cortex called *'ethological action maps'* (Graziano, 2015). However, it has not been confirmed that only kinematic components are the central element in this proposed scheme of organization of action representations.

Another way of organizing actions in the brain could be based on a continuous space reflecting semantic similarities between various categories. It has been argued that this kind of organization would enable a more efficient representation of the diversity of categories in a compact space, because semantically related action categories can share neural processes required to represent these actions (Huth et al., 2012). Studies investigating relations between objects, tools and actions have found that semantic knowledge about movements and semantic similarity between actions played a critical role in processing thematic relations (Buxbaum & Kalénine, 2010; Klatzky et al., 1993; Tsagkaridis, Watson, Jax, & Buxbaum, 2014; Watson & Buxbaum, 2014; Watson et al., 2013). Therefore, it has been suggested that organizing action representations in terms of their semantic similarity would be more efficient for dealing with a high number of actions, similar to the problem of representing numerous categories of different objects (Huth et al., 2012; Kriegeskorte, 2008; Lingnau & Downing, 2015; Pulvermüller et al., 2014; Pulvermüller, 2005; Watson & Buxbaum, 2014). These studies advocate the view of a *'semantic action space'* for the representation of different actions.

Our present results do not specifically favor any of the abovementioned views, but are consistent with the findings of previous studies underlining that semantic knowledge might play an important role as the organization principle of encoding different representations of social actions (Huth et al., 2012; Watson & Buxbaum, 2014). Why would semantic information play such an important role for the encoding of action representations? This seems plausible as different abstraction levels corresponding to action hierarchies appear necessary to form efficient, functional action representations (de la Rosa et al., 2015; Grafton & Hamilton, 2007; Uithol, van Rooij, Bekkering, & Haselager, 2012). In these action hierarchy models, semantic information has to be located at a higher hierarchical stage than kinematic information, since the motion of numerous different actions can converge into the same meaning of an action (e.g. handshake, high five, hug, fistbump could all have more different kinematic motions, but could be closer in their social everyday meanings). Previous studies have also confirmed that there could be multiple semantic interpretations for the same action, and that the perceived semantic meaning of an action was crucial for the categorization of an action (de la Rosa et al., 2014, 2015). These findings could potentially explain why action representations would be more robustly encoded with semantic information compared to kinematic information.

2.5.2. Representing the meaning vs. motion of an action

In the present study, we investigated kinematic information (motion) of an action opposed to the semantic information (meaning) of an action. But we could also critically review this comparison: Is the motion and the meaning of an action really encoded differently?

There is general agreement on what the motion of an action consists of – spatiotemporal changes in the limb positions during a performed action – but what is the meaning of an action? In previous studies, the meaning of an action has been generally recapitulated as understanding the intention or goal of a movement (Cavallo, Bucchioni, Castiello, & Becchio, 2013; Corbett & Enns, 2006; Grafton & Hamilton, 2007; Hamilton & Grafton, 2006; Loucks & Baldwin, 2009; McCabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2015; Prinz, 2014; Springer & Prinz, 2010). Although the exact definition of an action goal shows some variability in the literature, most studies agree that the goal of an action seems to be essential for action representations, and it has been even shown that great apes and young children already generate goal-based action predictions which are sensitive to the final goal of an action (Fogassi et al., 2005; Kano & Call, 2014; Olofson & Baldwin, 2011; Sommerville, Woodward, & Needham, 2005).

Recent studies showed that the intentions and goals of other people could be inferred from the movement kinematics of performed actions (Ansuini et al., 2014; Becchio et al., 2014, 2008a, 2010; Georgescu et al., 2014; Sartori et al., 2011). Other studies have shown that both the conceptual knowledge of action goals and physical movement goals can be recognized from performed actions of other people, although there are individual differences in recognition abilities (Ondobaka, de Lange, Newman-Norlund, Wiemers, & Bekkering, 2012; Ondobaka, de Lange, Wittmann, Frith, & Bekkering, 2014; Ondobaka, Newman-Norlund, De Lange, & Bekkering, 2013). There has also been evidence that not the motor movements per se are important but rather the action goal for carrying out these movements (Bianco et al., 2015; Umiltà et al., 2008). Recent studies of our group have also shown that reading and predicting the goal of an action is strongly modulated by the social context, and the same action consisting of identical motions can represent different semantic meanings (de la Rosa et al., 2015, 2014; Streuber, Sebanz, Knoblich, Bülthoff, & de la Rosa, 2011). Taken together, these results suggest that the kinematic and semantic information of actions are complementary and both integral components of the cognitive organization structure of action representations. Depending on what view one takes, one could interpret these findings both ways: That either semantic information about the meaning of an action is already grounded in the movements of an action – "so there can be no meaning without movement" (*Meaning-is-Embodied*) – or that kinematic information is already embedded in semantic conceptual knowledge about an action – "that there can be no movement without meaning" (*Movement-is-Symbolic*) (Prinz, 2014). The results of our experiments could be interpreted in the light of both views: that either a common motion template for the actions is exists and that different degrees in the distortion of this motion template would predominantly account for the modulation of meaning, or by assuming prior semantic knowledge of action concepts and interpreting the recognition of meaning as an activation of these concepts which is predominantly influencing the recognition of motion. However, these two views are not mutually exclusive and can also be interpreted as complementary to each other, since both views would agree that kinematic as well as semantic information about an action draw on common representations of actions.

2.5.3. Assessing visual processes underlying action representations

Our study adds novel insights to the ongoing discussion by using the experimental paradigm of adaptation aftereffects. The paradigm of high-level action adaptation aftereffects was our main choice of method in answering this question, because this methodology – also known as "the psychophysicists' electrode" (de la Rosa et al., 2014; Leopold et al., 2001) – has not been much used in the field of action recognition yet, and enables us to make inferences about the contribution of specific underlying neural populations (Clifford et al., 2007; Clifford & Rhodes, 2005; de la Rosa et al., 2014; Webster, 2011). Previous studies focusing on conceptual, semantic aspects of action knowledge often drew their conclusions from trying to connect language-related processes to action recognition and predominantly highlighting sensory-motor representations and motor resonance (Aziz-Zadeh et al., 2006; Glenberg & Gallese, 2012; Kiefer & Pulvermüller, 2012; Pulvermüller, 2005; Taylor et al., 2008; Zwaan & Taylor, 2006). These studies have put great emphasis on making the link from actions to languages. However, our study stands out by focusing on the underlying visual processes for action representations. Previous results from our group showed that exchanging visual stimuli of actions with action-related words did not directly result in congruent action adaptation aftereffects (de la Rosa et al., 2014), implying that there might be different processes involved in the processing of visual action representations. Nonetheless, the results of our present study are noteworthy, because we also arrive at similar conclusions that semantic knowledge of actions plays an important role for action recognition without initially focusing on the role of language in action representations. To our knowledge, the present study is the first trying to answer the question how different social actions are represented in the brain using an adaptation aftereffect paradigm.

2.5.4. Future directions

Although the two experiments in our present study consistently highlight the importance of semantic categorization for action recognition, a number of unanswered questions remain. First, it would be interesting to test whether these results generalize for a much higher number of actions. It has been pointed out that faces and actions have much in common, and in the research domain of face processing the idea of a “face space” has been successfully explored to investigate how different faces are represented in the brain (Leopold et al., 2001; Loucks & Baldwin, 2009). Following a similar approach to explore an “action space” in the brain with a much higher number of actions would contribute further insights to the discussion regarding the underlying organization principles for action representations. Second, another question for the future would be confirming the neuroanatomical correlates to the action adaptation aftereffects. Comparing the results of the study with other studies already existing in the field of neuroimaging would be valuable in order to narrow down possible neural mechanisms for the adaptation aftereffects and action representations (Freedman & Miller, 2008; Grafton & Hamilton, 2007; Hamilton & Grafton, 2006; Huth et al., 2012;

Lestou, Pollick, & Kourtzi, 2008; Lingnau & Downing, 2015; Miller, Nieder, Freedman, & Wallis, 2003; Ortigue et al., 2009; Schubotz, Korb, Schiffer, Stadler, & von Cramon, 2012; Wiggett & Downing, 2011). Open questions would be asking in which hierarchical manner these action representations are organized, and whether and how these action representations are distributed across different brain areas and functional systems (Giese & Rizzolatti, 2015; Grafton & Hamilton, 2007; Hamilton & Grafton, 2006; Lingnau & Downing, 2015; Van Overwalle & Baetens, 2009). The current experimental paradigm has a strong potential to serve as a useful method in this field for further mapping the relationship between different actions in the human brain.

2.5.5. Conclusions

The results of the present study demonstrate that both kinematic and semantic information play an important role for the organization of action representations. Using an action adaptation aftereffect paradigm, we showed that perceived differences between distinct social actions seem to be encoded both in terms of kinematic motion and their semantic meaning. We also created novel distorted actions with same degrees of kinematic distortion and different levels of semantic contents and showed that the emergence of an action adaptation aftereffect depended on recognized semantic contents. Our results highlight that semantic knowledge of an action is crucial for action recognition.

2.6. Acknowledgements

The authors like to thank Christian Wallraven and Michael Geuss for their valuable comments about this study as well as proofreading, and Tobias Meilinger, Stephan Streuber, Laura Fademrecht, Aurelie Saulton, Isabelle Buelthoff, Janina Esins for their support and discussions about the results, interpretations and conclusions.

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3 Cross-Cultural Action Recognition: A Comparison Study between Germany vs. Korea

The current chapter is based on the draft of an article which has been prepared for submission as a Brief Report to the Journal *Psychological Science*: "A Cross-Cultural Comparison of Social Action Recognition in Germany vs. Korea" by Dong-Seon Chang, Junsuk Kim, Uijong Ju, Stephan Streuber, Christian Wallraven, Heinrich H. Bülthoff and Stephan de la Rosa.

3.1. Abstract

The way social actions are used in everyday life to interact with other people differs across various cultures. Can this cultural specificity of social interactions be already observed in perceptual processes underlying the visual recognition of actions? We investigated whether there were any differences in action recognition between Western and East Asian cultures by testing German and Korean participants using questionnaires and a visual adaptation paradigm. First, both German and Korean participants had to recognize and describe four different social actions (handshake, punch, wave, fistbump) presented as brief movies of point-light-stimuli in an action naming task. Then, they had to rate similarities of actions in terms of their motion and meaning for all possible action pairs. Finally, we examined the underlying representations for each action using an action adaptation paradigm. Participants were repeatedly exposed to different action stimuli in separate experimental blocks. After being adapted in each experimental block, participants had to categorize ambiguous test stimuli in a 2-Alternatives-Forced-Choice (2AFC) task. The test stimuli were created by linearly combining the kinematic patterns of two actions such as a punch and a handshake. We measured the degree to which each of the four adaptors biased the perception of the subsequent ambiguous test stimulus for German and Korean participants. In the action naming task, the actions handshake, punch and wave were correctly recognized by both Germans and Koreans, but most Koreans failed to recognize the correct meaning of a fistbump. In the similarity rating task, both German and Korean participants showed highly consistent ratings. Also in the adaptation task, Germans and Koreans also showed remarkable similarities regarding the relative perceptual aftereffects induced by the adaptation to different action stimuli. In sum, our results imply a surprising consistency and robustness of action recognition processes across different cultures.

Keywords: Action, Adaptation, Cross-Cultural, Culture, Social Interaction

3.2. Introduction

Imagine a five-year old European boy from Germany visiting a foreign country in the Far East, Korea, for the first time in his life. When he sees a polite hotel doorman bowing almost 90 degrees, will he be able to grasp the meaning of this action correctly? Judging from his previous knowledge about the meaning of such movements, the boy might just think that the man is looking for a lost object – a key, or money – on the ground. On the other hand, judging from the context and the movements, the boy might intuitively understand that this bow was a form of greeting, since the movement was directed towards him and distinct from the ways people move when looking for a lost object.

This example illustrates an important question in the field of cultural psychology and cultural neuroscience: Are the cognitive processes underlying action recognition culture-specific or common across different cultures?

Cross-cultural comparison studies in the field of action recognition have been relatively rare. Classical cross-cultural studies have mainly focused on emotions asking whether the perception and communication of human emotions are universal or culture-specific (Chiao et al., 2010; Coetzee, Greeff, Stephen, & Perrett, 2014; Ekman, 1972, 1994; Ekman et al., 1987; Elfenbein & Ambady, 2002, 2003; Jack, Blais, Scheepers, Schyns, & Caldara, 2009; Matsumoto, 1992; Russell, 1994; Sauter, Eisner, Ekman, & Scott, 2010, 2015; Tanaka et al., 2010; Weisbuch & Ambady, 2008). These studies have investigated facial expressions (Chiao et al., 2008; Ekman, 1972, 1994; Elfenbein & Ambady, 2002; Jack et al., 2009; Weisbuch & Ambady, 2008), eye gaze (Adams & Kleck, 2003, 2005; Adams et al., 2010; Krämer et al., 2013), voices (Sauter et al., 2010; Tanaka et al., 2010) or body postures (Freeman, Rule, Adams, & Ambady, 2009; Tracy & Robins, 2008b) but only very few have looked at dynamic action stimuli (Bente, Dratsch, Rieger,

& Al-issa, 2014; Montepare & Zebrowitz, 1993) and cross-cultural studies of the recognition of social actions have been almost completely absent.

The way we use social actions in everyday life to interact with other people differs substantially from the ways we use to express emotions. Whereas perception of emotions from non-verbal expressions occur almost automatically (Tracy & Robins, 2008a, 2008b), the recognition of the meaning of social actions is a more complex predictive activity which requires more time and experience (Jeannerod, 1994; Jellema & Perrett, 2006; Lingnau & Petris, 2013; Springer, Hamilton, & Cross, 2012). It has been shown that a great amount of information is encoded in social actions and people do not only infer short-term movement goals from the kinematics of an action, but even intentions, personality traits (e.g. trustworthiness) or identity information about the person who performed the actions (Becchio, Sartori, & Castiello, 2010; DeSteno et al., 2012; Georgiou, Becchio, Glover, & Castiello, 2007; Loula, Prasad, Harber, & Shiffrar, 2005; Sartori, Becchio, & Castiello, 2011; Streuber, Sebanz, Knoblich, Bülthoff, & de la Rosa, 2011; Thoresen, Vuong, & Atkinson, 2012). Although the meaning of social actions also shows large variations across different cultures, whether and how people from different cultures differ in their perception and judgments of social actions have not been studied in detail yet.

Two cultures often studied in cross-cultural studies are Western and East Asian cultures, which are known to differ in many aspects, such as in low level visual perception, group behavior, social values etc. (Freeman, Rule, & Ambady, 2009; Han & Northoff, 2008; Han et al., 2013; Kitayama & Park, 2010). It has been reported that the way simple objects (e.g. lines) are perceived and represented in the brain already shows differences between East Asian and Western cultures (Hedden, Ketay, Aron, Markus, & Gabrieli, 2008; Kitayama, Duffy, Kawamura, & Larsen, 2003). It has been also shown that that East Asians are tending more towards holistic perception integrating contextual information in objects and scenes and Western societies emphasize individualistic thinking more resulting in perception of distinct parts of objects and scenes ignoring contextual information (Freeman, Rule, & Ambady, 2009; Miyamoto, Nisbett, & Masuda, 2006; Nisbett, Peng, Choi, & Norenzayan, 2001). In addition, the values of the societies guiding group behavior shows fundamental differences between East Asian and Western cultures, the former known to be promoting more collectivistic, and the latter more individualistic behavior (Freeman, Rule, & Ambady, 2009; Han & Northoff, 2008; Han et al., 2013). The way social actions are used also show distinct differences between both cultures. For example, people in Western cultures greet each other more directly from person to person, e.g. with a handshake or high five. People in East Asian cultures often use greetings that can be directed towards one person as well as multiple persons, e.g. with a bow, or waving with the hands. In addition, negative actions such as attacking another person are condemned stronger in East Asian cultures, being required to hide and not openly show individual conflicts.

In the present study, we wanted to compare the cognitive processes underlying the recognition of social actions in different cultures. For this, we compared Western and East Asian cultures and tested participants from Germany and Korea, because cultural differences between these cultures were well known. We first examined the way people describe an action and how they compare different actions with each other by an action naming task and similarity rating task. We used four different actions – handshake, punch, wave and fistbump – as our stimuli, especially the action fistbump was chosen because the meaning of this action was unknown to most East Asian cultures. Second, we wanted to investigate whether the cultural specificity known from everyday life social interactions can also be observed in perceptual processes underlying the visual recognition of actions. Here, we used an action adaptation paradigm and compared the action adaptation aftereffects to each social action in German and Korean participants. In sum, we wanted to investigate whether there were any differences in action recognition processes between participants from Germany and Korea.

3.3. Materials and Methods

3.3.1. Participants

We recruited 24 participants from Germany (mean age = 29.34 ± 7.08 years, female = 15, male = 9) and 24 participants from Korea (mean age = 23.08 ± 8.92 years, female = 11, male =13) for the experiment. Participants from Germany were recruited from the local community using the Tübingen MPI subject database, and participants from Germany were recruited from the local college community at Korea University in Seoul. All participants had normal or corrected-to-normal stereoscopic vision and normal hearing. They were all naïve concerning the hypotheses of the experiment, and were appropriately informed about the general purpose of the experiment prior to signing the informed consent. All participants received 8 €/hour as a compensation for the participation in the experiment. The experiment was conducted in line with the Declaration of Helsinki and in accordance with the recommendations of the ethics board of the University of Tübingen and Korea University.

3.3.2. Stimuli and Apparatus

We recorded different social actions using a motion capture suit equipped with 17 inertial motion trackers distributed over the whole body (MOVEN Motion Capture Suit from XSense, Netherlands). The stimuli and apparatus, design and procedure of the present experiment followed exactly the same as previously described in Chang et al., 2016 (In the current dissertation described in Chapter 2: Motion vs. Meaning). We used four different social actions as our stimuli: handshake, wave, punch and fist bump, presented from the side view. All actions were cut and processed into standardized short movies of point-light-dot stimuli (Johansson, 1977), only showing the movements of the joints (number of joints shown = 15; number of frames = 160, refresh rate = 120 frames per second (fps)). The adaptor stimuli were each of the four actions presented in separate experimental blocks. The test stimuli were action morphs between two actions (handshake and punch) generated by taking the weighted average linear distance between the joint positions in space for each recorded frame of an action. Morph weights were determined in pilot trials measuring the point when participants reported overall ambiguous perception for the two morphed actions. We used eight different morph weights between two actions ranging from 0% of action 1 until 100% of action 2 (morph weights: 0, 0.3, 0.6, 0.67, 0.73, 0.8, 0.9, 1). The test stimuli consisting of morphed actions were 18 times repeatedly presented in each adaptor block, whereas the presentation order of different morph weights were completely randomized (i.e. psychophysical method of constant stimuli). All stimuli were presented on a LCD monitor (refresh rate of 60 Hz; screen resolution of 1280 x 1024 pixels) using MATLAB and Psychophysics Toolbox.

3.3.3. Procedure

All participants carried out 1) an action naming task, 2) similarity rating task, and 3) different blocks of an adaptation experiment in a fixed order.

<u>Naming Task:</u> First, participants were presented with each of the four different social actions – handshake, punch, wave, fist bump – and had to name and describe each action how they perceived it.

<u>Similarity Rating Task:</u> Subsequently, participants were presented all possible pairs of the four social actions and had to rate how they perceived pairwise similarities of the four actions in terms of kinematic motion (“How different do the motion trajectories of the body parts and joints in these two actions appear? Think in terms of similarities or differences in the movements you need to carry out for performing these two actions.”), and in terms of semantic meaning (“How different do the meaning of these two actions appear? Think in terms of similarities or differences how these actions are used in social

situations.”). The ratings were collected on a visual analogue scale ranging from 0 (exactly same) to 10 (completely different).

Main Adaptation Experiment: The main adaptation experiment consisted of five experimental blocks, always starting with a block of trials where participants watched all test stimuli without the presentation of an adaptor in order to measure participants’ perception of the test stimuli without adaptation (baseline). The following four experimental blocks of trials each probed a different adaptor (handshake, punch, wave, fist bump), and the order of these blocks were completely balanced across all participants. Each experimental block consisted of a total 144 trials (8 different morph levels x 18 randomized repetitions of test stimuli). Each block started with an initial adaptation phase consisting of 30 presentations of the adaptor stimulus (inter-stimulus-interval (ISI) = 200 milliseconds), then experimental trials began. On each trial, three repeated presentations of one adaptor stimulus were followed by a test stimulus presented on a screen and participants had to judge which action they recognized (e.g. “Did you see a handshake or a punch?”) in a 2-alternative-forced-choice (2AFC) task. The ISI between the adaptor stimuli and test stimuli were 100 milliseconds, and a beep tone always preceded the presentation of the test stimuli. The next trial started as soon as the participants gave the answer by pressing a button on the keyboard. The total number of trials for each participant was 720 trials (5 experimental blocks x 8 different morph levels x 18 randomized repetitions of test stimuli). Participants took 5-10 minutes breaks between each experimental block. After the whole experiment, the participants filled out a feedback questionnaire with general questions about the experiment.

3.3.4. Data Acquisition and Analysis

All participants’ answers for the naming task and action similarity/difference rating were translated from German and Korean into English to enable objective comparisons. The correct recognition rate for each action was computed on the basis of whether the descriptions matched the originally intended action carried out during the action recordings. Because the presented stimuli were impoverished in terms of their naturalness (i.e. point-light-stimuli), and some of the actions were generally unknown to Koreans (and in East Asian cultures), a correct description of all actions in the naming task could not be expected by default. We performed a post hoc categorization of all translated action descriptions in terms of their valence (positive, neutral or negative) and socialness (directed to a person or not), in order to make sure that the translated description of the actions carried the same meaning. For example, if someone described an action as "Tapping on the shoulder to cheer up the other person", this means that the person perceived the action as positive (positive valence) and directed at another person (social), even when the person did not correctly recognize the stimulus as "an activity of greeting by bumping two fists". This post hoc categorization for valence and socialness was carried out by six different independent raters (3 Germans, 3 East Asians) whereas we took the median value of all six different ratings. All data collected during the main adaptation experiment was automatically saved by MATLAB and the Psychophysics toolbox. The adaptation aftereffects for each social action were computed by fitting a psychometric function to each participant's data describing the proportion of 'punch' responses in each adaptor block as a function of the morph levels of the presented test stimuli. We used a Weibull function with α (position of the psychometric function along on the x-axis) and β (slope of the psychometric function), and γ (lapse rate) as free parameters (gamma was fixed to 0), following the same analysis procedure as in our previous studies (de la Rosa, Streuber, Giese, Bülthoff, & Curio, 2014). From the psychometric functions, we determined the point of subjective equality (PSE) – the morph level where participants gave an equal amount of 'punch' and 'handshake' answers – for each participant and adaptor block. The adaptation aftereffects for each action stimuli were defined as the PSE differences between each adaptor and baseline condition.

3.4. Results

3.4.1. Action Naming Task

We compared all German and Korean participants' answers how they described the perception of each social action shown as point-light-stimuli. The correct recognition rate of the actions handshake, punch, wave and fist bump was compared between German and Korean participants. The actions handshake, punch and wave were correctly recognized by the majority of both Germans and Koreans, and a Chi-squared-test revealed no significant differences in the recognition rate between Germans and Koreans for the actions handshake, punch or wave. However, Koreans (M = 58.3%) in comparison to Germans (M = 100%) showed a significantly lower recognition rate for the action fist bump, ◎2(1, N=24) = 10.23, p = 0.001 (see Figure 3-1).

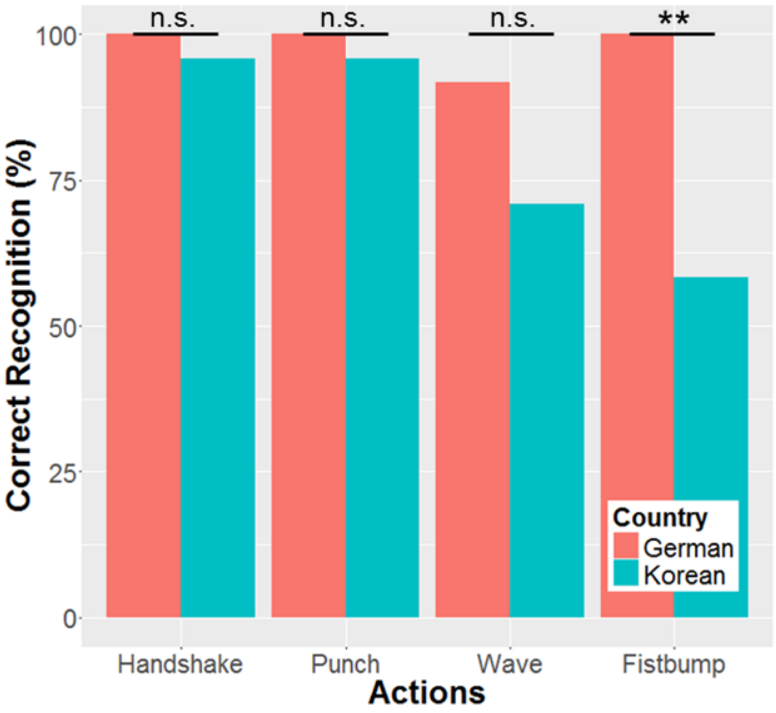


Figure 3-1. Comparison of Recognition Rate. The correct recognition rate for actions shown as brief movies of point-light-stimuli in an action naming task was compared between German and Korean participants. The mean recognition rate of the actions Handshake, Punch, Wave, Fist bump were 100%, 100%,91.67%, 100% for German (n=24), and 95.83%, 95.83%, 70.83%, 58.33%, respectively, for Korean participants (n=24).

3.4.2. Action Similarity Rating Task

We compared German and Korean participants' action similarity ratings of the four actions in terms of their perceived similarity or differences in kinematic motions and semantic meanings. To compare German and Korean participant's ratings, we performed a multivariate analysis of variance (MANOVA) on the similarity ratings of the both groups Korea and Germany and the two dependent outcome variables motion similarity and meaning similarity ratings. There was no significant effect of culture on the motion or meaning similarity ratings ($F(2,285) = 2.11$, $p = 0.12$). The action similarity ratings of all participants showed high internal consistencies with a Cronbach's alpha of $\alpha = .98$ for Germany, and $\alpha = .94$ for Korea, as well as $\alpha = .97$ for all twelve action pair rating items across all rating categories, and high inter-rater-reliabilities with an intra-class correlation coefficient (ICC) of rICC = 0.742 for German, and rICC = 0.403 for Korean participants, and rICC = 0.579 across both populations and rating categories (see Figure 2B). When both ratings categories were compared, the inter-rater-reliabilities were lower for ratings of motion (Germany: rICC = 0.524, Korea: rICC = 0.284 Overall rICC = 0.377) than for meaning (Germany: rICC = 0.878, Korea: rICC = 0.536, Overall rICC = 0.72). The internal consistencies and inter-rater-reliabilities of the action similarity ratings showed high similarities between German and Korean participants (see Figure 2B, for more data, see Supplementary Material). The overall action similarity ratings of German and Korean participants were also highly correlated with a Pearson correlation coefficient of $r = 0.917$, $p < 0.001$, 95% CI (0.723, 0.977) (see Figure 2C). When ratings categories were compared with each other, the motion ratings did not show a significant correlation ($r = 0.728$, $p = 0.101$), but the meaning ratings of German and Korean participants showed a strong correlation ($r = 0.989$, $p < 0.001$) (see Supplementary Material). A linear regression analysis showed that German ratings of overall action similarity significantly predicted the Korean ratings, with $\beta = .63$, $t(10) = 7.25$, $p < 0.001$, and with a large effect size of $R2 = .82$, $F(1,10) = 52.58$, $p < 0.001$.

3.4.3. Post Hoc Categorization of Action Descriptions

Six independent raters categorized each participant's action descriptions in the naming task post hoc in terms of their expressed valence and socialness. The six different independent raters showed high consistency (Cronbach's α=.91) and high inter-rater-reliability (average ICC=.86) in rating the answers. There were no differences in the categorization of actions in terms of their valence or socialness (see Supplementary Material).

3.4.4. Action Adaptation Aftereffects

The adaptation aftereffects for the different social actions were very similar for both cultures (see Figure 3). An analysis of variance with the PSE values (alpha) revealed a significant main effect for adaptor actions $F(3,138) = 54.19$ $p < 0.001$, but not for culture, and without a significant interaction between adaptor action and culture. An analysis of variance with the slopes (beta) of each action also revealed a significant main effect for adaptor actions $F(3,138) = 9.69$, $p < 0.001$, but not for culture, without a significant interaction. Also, a post-hoc t-test comparison for the adaptation aftereffects of the action fistbump revealed no significant differences between Germans and Koreans, neither for the PSE value (alpha) $t=0.799$, $p = 0.428$, nor for the slope (beta) $t=1.708$, $p = 0.094$. However, the data of Germans and Koreans demonstrated remarkable similarities in the patterns and magnitudes of the visual action adaptation aftereffects, showing a strong correlation ($r = 0.97$, $p < 0.01$), regardless of whether we compared the slope or the PSE of the psychometric curves.

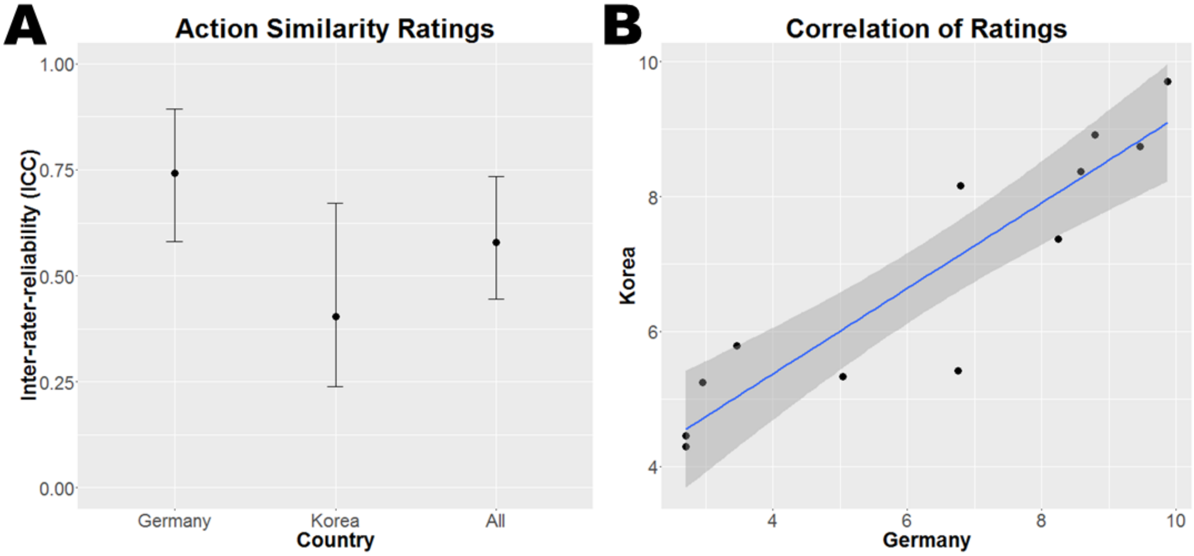


Figure 3-2. Comparison of Action Similarity Ratings. A: The inter-rater-reliabilities of the actions ratings were computed as the intra-class-correlation coefficient (ICC) of each group (Country) and across both groups and rated categories (motion or meaning). Error bars indicate the standard error of the mean. **B:** The German average of action similarity ratings for all action pairs was correlated with the Korean average of action similarity ratings for all action pairs. The correlation was significant, with a correlation coefficient of $r = 0.917$, $p < 0.001$.

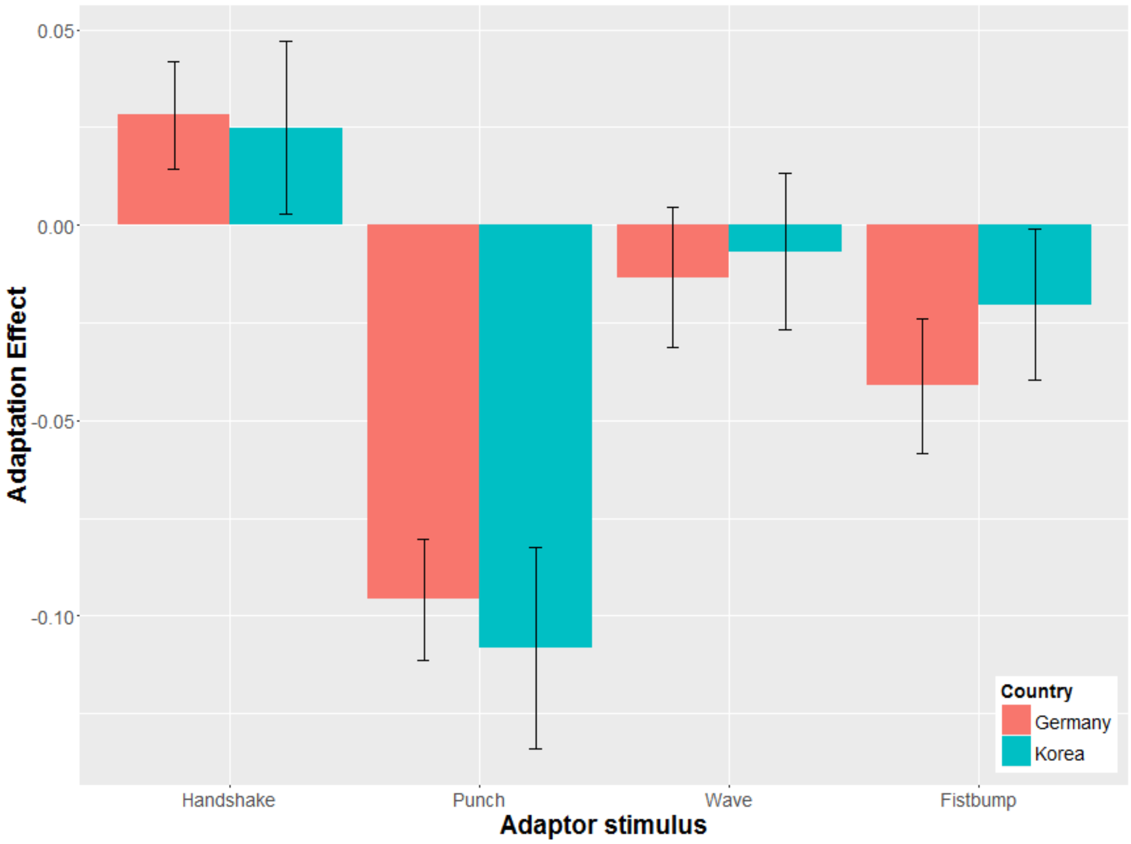


Figure 3-3. Comparison of Action Adaptation Aftereffects. The measured adaptation aftereffects showed very consistent and similar patterns across German and Korean participants, showing no significant differences between both cultures. The error bars show the standard error of the mean.

3.5. Discussion

The main aim of the present study was to investigate whether there were any differences in social action recognition processes across two different cultures. We showed four different actions – handshake, punch, wave, fistbump – as brief movies of point-light-stimuli to participants from Germany and Korea. In an explicit action naming task, all actions were equally well recognized in both countries, except for the action fistbump (see Figure 3-1). A MANOVA on the action similarity ratings showed no significant differences between both countries, and the pairwise similarity ratings of all actions in terms of their perceived motion and meaning showed high consistencies and interrater reliabilities between participants from Germany and Korea, with a high correlation between both cultures (see Figure 3-2). The measured action adaptation aftereffects for each of the actions also showed no significant differences between German and Korean participants neither for the PSE nor for the slopes of the fitted psychometric curves for all actions (see Figure 3-3 and Supplementary Material). In sum, we found no significant differences in the processes underlying social action recognition between German and Korean participants, although one of the actions, fistbump, was almost completely unknown to the Korean culture, as shown in the explicit action naming task.

The overall consistency in the action similarity ratings between German and Korean participants is striking (see Figure 3-2). The overall pattern of similarity ratings were both highly reliable across different raters (Figure 3-2A), and also highly correlated between the two different cultures (Figure 3-2B). Even more surprising was the fact that the measured action adaptation aftereffects were also very similar and showed no significant differences overall (Figure 3-3). The non-existing difference particularly for the action fistbump was puzzling, since this action was unknown in one culture but well known in another. However, when we looked at the post-hoc categorization data of the descriptions of the action fistbump carried out by the six independent raters, the described content was rated mostly similar in terms of their valence and socialness. In other words, although participants from Korea were not able to correctly recognize and name the action fistbump, it seems most of them experienced a similar perceived valence and socialness from the observation of this action. This could explain the similar adaptation effects for the action fistbump regardless of culture. In sum, it seems that the underlying processes to social action recognition are highly robust and consistent even across such different cultures as Western and East Asian cultures.

How can we explain the overall similarity in the underlying processes for social action recognition between German and Korean participants? One possibility is that the perceptual processes underlying the visual recognition of actions are specifically tuned to the motion kinematics of actions which are perceived robustly and consistently, regardless of whether one can explicitly name or describe an action or not. Previous research on action recognition would support this explanation as it has been shown that humans can consistently interpret the underlying intentions in actions based on the motion kinematics of the actions carried out (Becchio et al., 2014; Becchio, Sartori, Bulgheroni, & Castiello, 2008; Georgiou et al., 2007; Manera, Schouten, Becchio, Bara, & Verfaillie, 2010). For example, the motion energy of the action fistbump might have contributed to the interpretation of the action as friendly and positive. The overall post hoc categorization data of independent raters supports this explanation as well, since all six raters were highly consistent in the interpretation of the qualitative descriptions of the Korean participants in terms of valence and socialness. In these data, the action fistbump was also consistently rated as positive and social (see Suppl. Data).

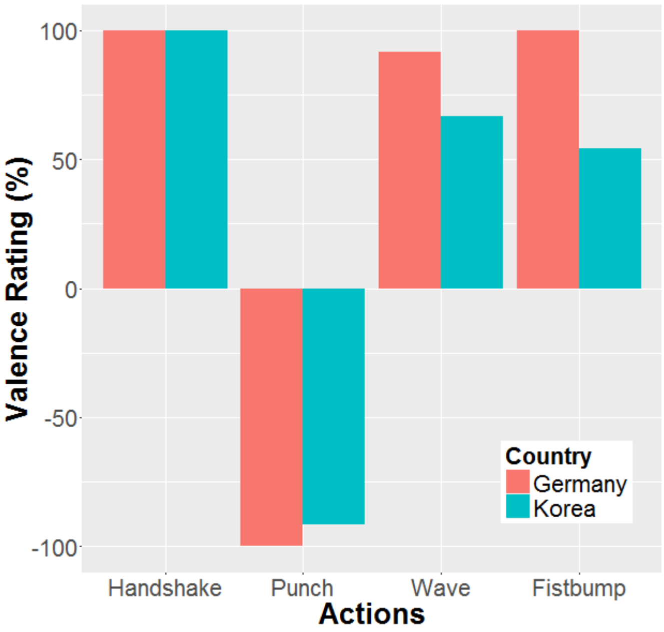
From an evolutionary point of view, it makes sense that processes underlying action recognition processes are highly robust and consistent even across different cultures, because the physical action effects mainly matter for survival, regardless of how they are named. Previous studies have reported that reading and interpreting the actions of other individuals played an important role in the evolution of the human brain and its intelligence (Adolphs, 2001; Dunbar, 1998, 2003; Frith & Frith, 2006; Tomasello, Carpenter, Call, Behne, & Moll, 2005). In this context, correctly interpreting the actions of other individuals in terms of their valence and intentions might be of such importance that there should be no big differences across different cultures.

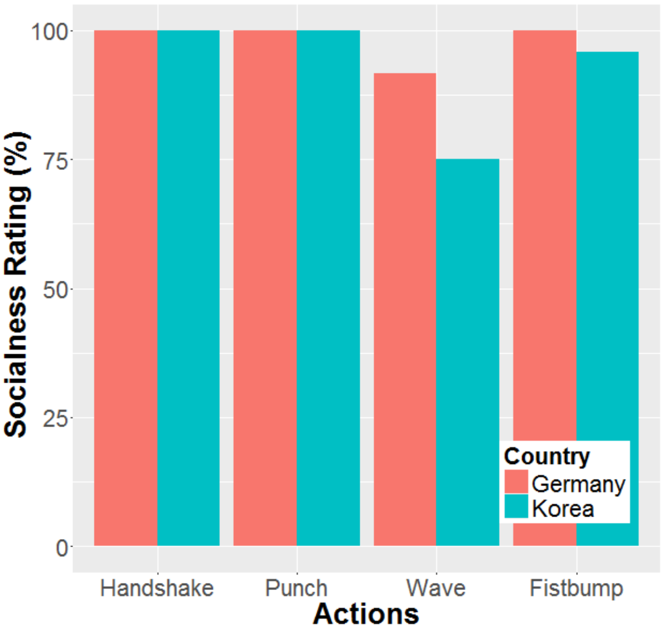
In sum, results of our present study show a surprising consistency and robustness of action recognition processes across different cultures. There have not been many cross-cultural studies in the field of action recognition, and our study is one of the first investigating the question whether perceptual processes underlying the visual recognition of social actions are culture-specific or common across different cultures. Future studies could test a higher number of different actions, and also other different cultures than Western or East Asian cultures. Moreover, combining adaptation aftereffect studies with neuroimaging approaches to investigate whether the neuroanatomical processes underlying social action recognition are also similar across different cultures would be definitely an interesting task for the future. Taken together, if a five-year old European boy encounters a novel action in Asia such as a polite bow, there is a high chance that he will intuitively grasp the meaning of this action correctly, just based on the movement patterns he observes. In sum, we conclude that common processes seem to underlie social action recognition processes across different cultures.

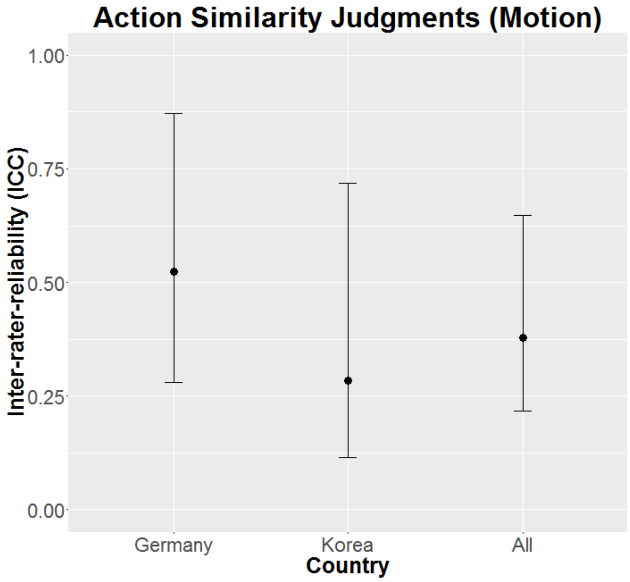
3.6. Acknowledgements

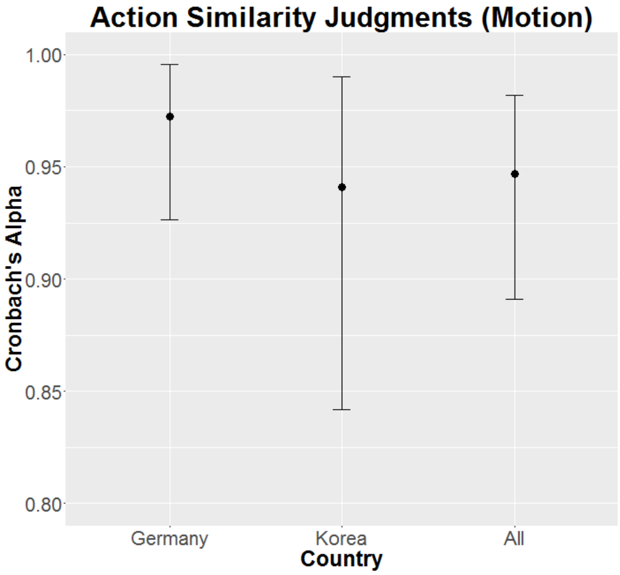
We thank Duangkamol Srismith, Mengying Zhang, Mintao Zhao, Laura Fademrecht, Thomas Hinterecker and Anne Thaler for their ratings of action descriptions in terms of valence and socialness. We also thank members of the Dept. of Brain & Cognitive Engineering at Korea University, Seoul, Korea, for their help in collecting Korean data, and members of the Social & Spatial Cognition Group at the MPI for Biological Cybernetics, Tuebingen, Germany, for their support.

3.7. Supplementary Material






Action Similarity Judgments (Motion)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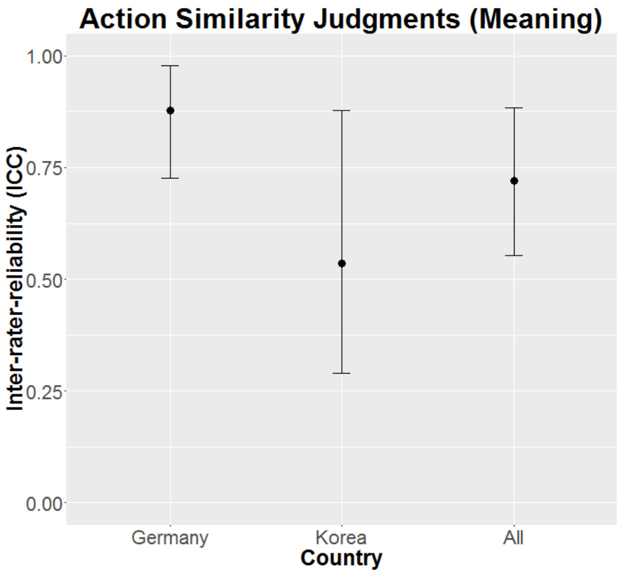
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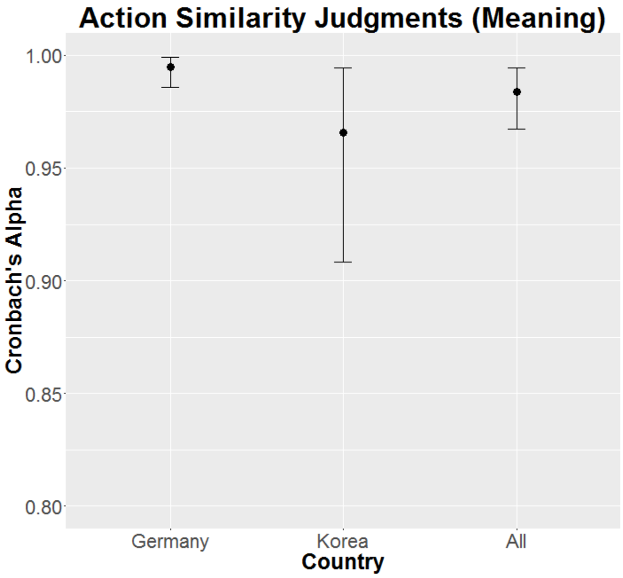
Action Similarity Judgments (Meaning)

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4 Visual Adaptation to Actions in Social Interactions: Evidence for Shared Representation of Actions

The current chapter is based on the draft of an article which has been prepared for submission as a Brief Report to the Journal *Current Biology*: "How your actions are coupled with mine: Evidence for shared representation of actions in the context of social interactions" by Dong-Seon Chang[*], Leonid Fedorov[*], Martin A. Giese, Heinrich H. Bülthoff and Stephan de la Rosa[*] (equal contributions indicated by asterisk *).

4.1. Summary

Social interaction plays a central role in human life. The extent to which humans can coordinate actions with other individuals is extraordinary amongst all social animals and the result of a long evolutionary path. The mechanism behind the ability for successful interactions is based on shared neural processes in the brain which are concurrently activated in interacting partners. Previous research has shown that humans share numerous underlying cognitive processes when they interact, such as representations of tasks, goals, intentions, and space. However, little is known about how humans encode the representations for specific actions in the context of an interaction. Are action representations in a dyadic interaction individually encoded for each person's action, or are they coupled so that complementary actions are encoded together?

Here, using a visual adaptation aftereffect paradigm we measured underlying action representations of dynamic human actions recorded from real life dyadic interactions. We found that prolonged viewing of an action (e.g. giving) induces also an adaptation aftereffect for the complementary action performed by the interaction partner (e.g. taking). There were no significant differences in whether the complementary actions were of “initiating” (giving, throwing) or “responding” (taking, catching) nature. These findings demonstrate for the first time that representations of actions are not individually encoded but shared in the context of dyadic social interactions. Such co-representations of actions may provide an effective anticipatory mechanism for humans to understand others’ actions and to engage in more complex social interactions.

Keywords: Action, Adaptation, Co-Representation, Joint action, Social interaction

4.2. Introduction

There is a famously recurring action scene in a number of martial arts movies. The protagonist, a martial arts master, is approached by attacking enemies and suddenly throws a random object (e.g. a ball) to them. To their own embarrassment, the enemies end up performing a perfect catch of this thrown object instead of carrying out their initial action plan of attacking the protagonist. There are similar cases observed in everyday life as well. When a ball is suddenly thrown to a randomly passing person most people will almost automatically catch the ball. The same will also happen if you try to give an object (e.g. a book) to a random person who is not prepared for this. Most people will take this object and only moments later wonder what they should do with this. Why did people carry out these actions then, although they did not initially plan to catch the ball, or take the book?

One explanation about this phenomenon comes from previous research on social perturbation stating that actions are intrinsically linked to perception and that observation of other people's actions almost automatically activate the same representations of these actions in oneself through predictive mechanisms (Kilner, Friston, & Frith, 2007; Kilner, Hamilton, & Blakemore, 2007; Kilner, Paulignan, & Blakemore, 2003). Several studies have found similar kinds of interference effects in action selection and execution induced by the observed actions of other people (Ferri, Campione, Volta, Gianelli, & Gentilucci, 2011; Sartori, Becchio, Bulgheroni, & Castiello, 2009), sometimes even induced by the mere presence of other people performing a similar task (Sebanz, Knoblich, & Prinz, 2003, 2005). Interestingly, these action interference effects have been found not only for similar and imitative actions (Kilner, Hamilton, et al., 2007; Kilner et al., 2003), but also for complementary actions (Sartori et al., 2009; Sartori, Betti, & Castiello, 2013; Sartori & Betti, 2015), and in some cases dependent on the action context (Sartori, Cavallo, Bucchioni, & Castiello, 2011). In general, these studies conclude that the visual perception of actions affording a social interaction would almost automatically trigger similar or complementary actions as a response, because the representations for these actions are coupled together in dyadic social interactions (Becchio, Manera, Sartori, Cavallo, & Castiello, 2012; Ferri et al., 2011; Gangopadhyay & Schilbach, 2012; Schilbach et al., 2013).

Another line of evidence for the coupling of actions observed in dyadic social interactions comes from visual recognition studies of social interactions (de la Rosa, Fuller, & Bülthoff, 2014; de la Rosa, Streuber, Giese, Bülthoff, & Curio, 2014; de la Rosa et al., 2015; Manera, Becchio, Schouten, Bara, & Verfaillie, 2011; Manera, Del Giudice, Bara, Verfaillie, & Becchio, 2011; Manera, Schouten, Verfaillie, & Becchio, 2013; Neri, Luu, & Levi, 2006). It has been shown that visual categorization of social interactions depend on the perceived social context and that sequences of actions performed by two interaction partners are interpreted together according to their semantic meanings (de la Rosa, Streuber, et al., 2014; de la Rosa et al., 2015). Moreover, it has been demonstrated that the actions of one person can reliably predict the actions of another person by enhancing the visual detection and discrimination of the second responding action (Becchio et al., 2012; Manera, Becchio, et al., 2011; Manera et al., 2013; Neri et al., 2006). This phenomenon has been explained by the dynamic coupling of actions in social interactions "enabling predictive coding in visual information retrieval" (Manera, Becchio, et al., 2011; Neri et al., 2006) which has been lately termed as 'interpersonal predictive coding' (Manera, Becchio, et al., 2011; Manera et al., 2013; Oberwelland et al., 2016). One can also explain the coupling of actions by the contingency between the actions induced by associative learning, due to the accumulation of previous observations of the spatiotemporal proximity of complementary actions (Cook, Bird, Catmur, Press, & Heyes, 2014; Cooper, Cook, Dickinson, & Heyes, 2013a). Taken together, previous research indicates that actions in the context of social interactions are dynamically coupled with each other, sharing underlying representations.

How are actions in the context of dyadic social interactions represented in the brain? Although much has been theorized about whether humans encode representations of other's actions in a similar way to how they encode their own actions, and whether the same neural circuits in the brain are involved for processing the information about one's own and others' actions (Iacoboni et al., 2005; Kokal, Gazzola, & Keysers, 2009; Newman-Norlund, Noordzij, Meulenbroek, & Bekkering, 2007; Pfister, Dignath, Hommel, & Kunde, 2013; Rizzolatti & Craighero, 2004; Sartori & Betti, 2015; Sebanz et al., 2003, 2005; Wenke et al., 2011), hard evidence showing whether representations of individual actions are really coupled and shared in the context of social interactions has been lacking.

Here, using a visual adaptation paradigm, we directly measured the underlying representations of complementary actions in the context of dyadic social interactions. We recorded two pairs of complementary actions from real life human interactions – "Giving" and "Taking" (Interaction 1), and "Throwing" and "Catching" (Interaction 2) – and assessed whether prolonged viewing of each action from these interactions induced an adaptation aftereffect (see Figure 4-1A, 4-1B). In an adaptation paradigm, participants view an adaptor stimulus (e.g. "Giving") repeatedly for a prolonged time and give answers to a perceptual categorization task with ambiguous test stimuli (e.g. Different morphs between "Giving" and "Throwing") (Figure 4-1C, 4-1D). Because prolonged exposure to one stimulus results in specifically decreased responses for the adaptor stimulus, participants will then also perceive less of the adaptor stimulus (e.g. give more answers for "Throwing") after adaptation. Since adaptation aftereffects measure the response changes of the underlying neural channels specifically tuned to the properties of the adaptor – which is why adaptation paradigms are even called the "psychophysicist's electrode" (de la Rosa, Streuber, et al., 2014; Leopold, O'Toole, Vetter,

& Blanz, 2001) – adaptation paradigms offer a useful method to examine the behavioral correlates of the underlying neural representations for the adaptor stimulus (Armann, Jeffery, Calder, & Rhodes, 2011; Barraclough & Jellema, 2011; Barraclough, Keith, Xiao, Oram, & Perrett, 2009; Clifford & Rhodes, 2005; Clifford et al., 2007; de la Rosa, Ekramnia, & Bülthoff, 2016; de la Rosa, Ferstl, & Bülthoff, 2016; de la Rosa, Streuber, et al., 2014; Leopold et al., 2001; Troje, Sadr, Geyer, & Nakayama, 2006; Webster, 2011).

In the current study, we took advantage of this specificity of the adaptation paradigm to answer the following particular question: Are representations underlying actions in the context of dyadic social interactions shared across complementary actions, or are each individually performed action represented separately? For this, we measured visual adaptation aftereffects for the actions “Throwing” and “Giving” after prolonged exposure to the actions “Catching” and “Taking”, and vice versa, in a completely crossed design (see Figure 4-1C). We wanted to see whether adaptation aftereffects were induced not only for each action (Normal-Adaptation) but for the complementary actions as well (Cross-Adaptation). Since the physical properties of all adaptor stimuli – “Giving”, “Taking”, “Throwing”, and “Catching” – were distinct from each other (and also semantically recognized as different actions), one should find no adaptation aftereffect for the complementary actions if representations for each action are encoded separately. However, if representations for actions in the context of dyadic social interactions are indeed coupled within each interaction, significant adaptation aftereffects should be observed for the complementary actions as well – e.g. adaptation aftereffects to “Throwing” induced by “Catching” – indicating shared representation of actions in the context of social interactions.

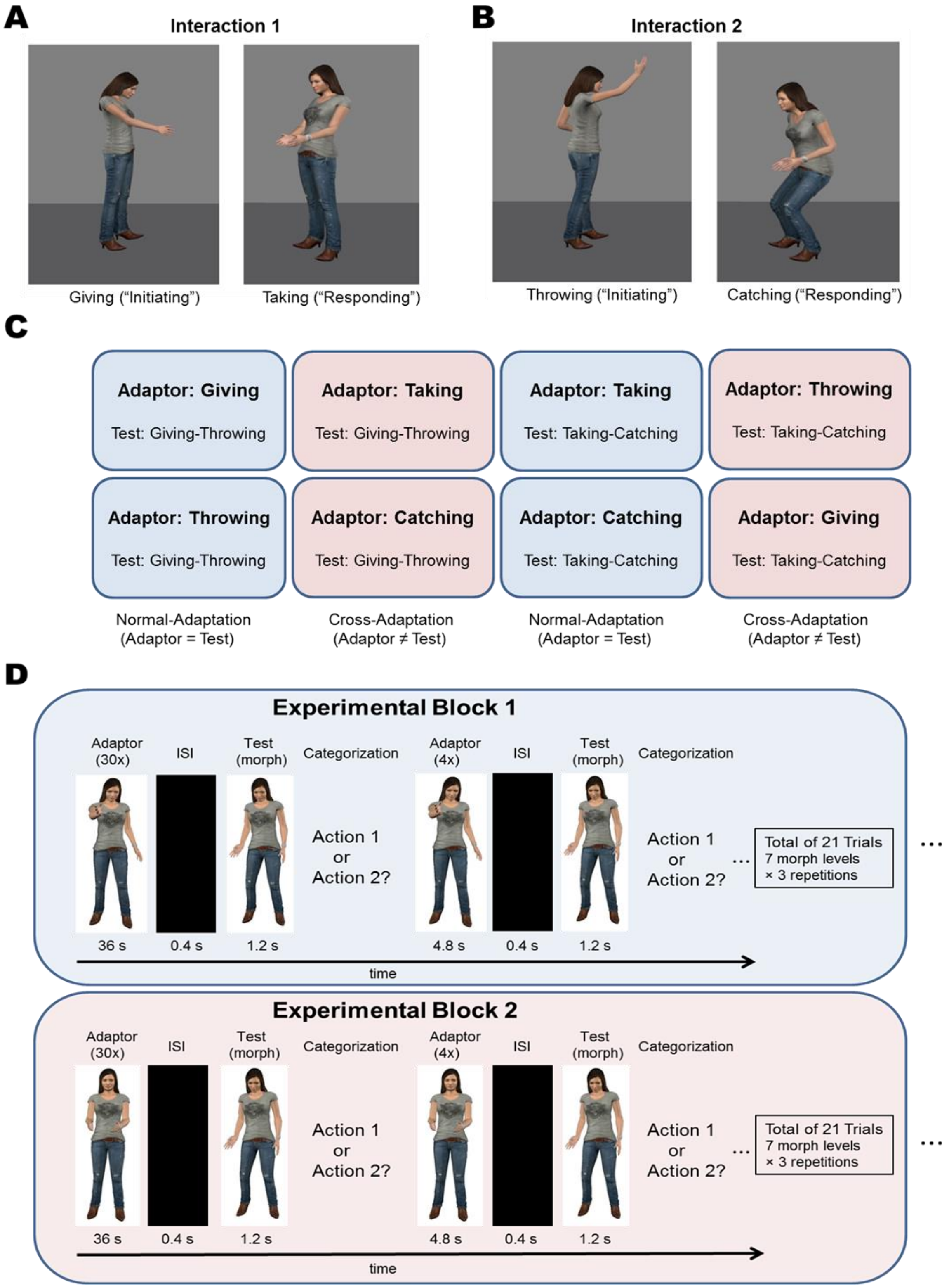

Figure 4-1. Examples of Stimuli, Design and Paradigm. A: The actions "Giving" and "Taking were recorded from Interaction 1. **B:** The actions "Throwing" and" Catching" were recorded from Interaction 2. **C:** Overview of all experimental blocks, following a completely crossed design, each consisting of a unique combination of adaptor and test stimuli. **D:** Examples of the adaptation procedure in each experimental block. Shown pictures are only snapshots and real stimuli were videos.

4.3. Materials and Methods

4.3.1. Subjects

A total number of 25 subjects (mean age = 26.3 years, standard deviation = 6.18; female = 14, male = 11) participated in the experiment who were recruited from the local community using the Tübingen MPI subject database. Inclusion criteria were that all participants had normal or corrected-to-normal stereoscopic vision. Exclusion criteria applied to participants who could not perceive the action stimuli with the 3D-goggles, who showed inconsistent responses after three iterations in the process determining the point of overall ambiguous perception for the two morphed actions (i.e. point of subjective equality; PSE), or who reported to have had extensive trainings in sports involving throwing or catching actions (e.g. experts in baseball, basketball, juggling). All participants were informed about the purpose of the experiment before signing an informed consent. All participants were naïve concerning the hypotheses of the experiment. They received 8 €/hour as a compensation for their participation in the experiment. The experiment was conducted in line with the Declaration of Helsinki and in accordance with the recommendations of the ethics board of the University of Tübingen.

4.3.2. Stimuli and Apparatus

We recorded the action stimuli from real life dyadic interactions using two motion capture suits each equipped with 17 inertial motion trackers distributed over the whole body (MOVEN Motion Capture Suit from XSense, Netherlands). Two actors were standing facing each other and carried out the actions starting from a neutral pose. We recorded two different sets of interactions between the actors: Interaction 1 (“Giving-Taking”) consisted of one person giving a small bag to another person who was taking it, and Interaction 2 (“Throwing-Catching”) consisted of one person throwing a small bag to another person who was catching it. From the two sets of naturally carried out dyadic interactions, four actions were recorded: “Giving”, “Taking”, “Throwing”, and “Catching”. The recorded action stimuli contained the information about the change of three-dimensional (3D) spatial coordinates of 22 body joints over time. All actions were processed into short movies of standardized lengths (1.2 s) by the morphing algorithm. We also generated ambiguous action morphs between actions originating from Interaction 1 or Interaction 2, whereas actions were either morphed between “initiating” actions (“Giving–Throwing” morphs) or “responding” actions (“Catching–Taking” morphs). The morphs were calculated by the weighted average of local joint angles between two actions. The morph levels were determined individually in practice trials (see Procedure). All stimuli were presented on an augmented reality setup where participants could see the actions in 3D and carried out by a real life size female avatar (height = 1.73 m). All actions were presented with the avatar facing the viewer at a fixed distance of 2.3 meters from the screen to the tracked glasses. The avatar kept a neutral facial expression. The setup was programmed and controlled with the Unity game engine (San Francisco, USA), and the animated avatar stimuli were acquired from Rocketbox (Hannover, Germany). The stimuli were projected using back-projection technique enabled by a Christie Mirage S+3K stereo projector (Kitchener, Canada) with a refresh rate of 101 Hz, and all participants wore Nvidia 3D Vision Pro shutter glasses (Santa Clara, USA) synchronized to the display in order to perceive the stimuli in 3D. An ART Smarttrack system (Weilheim, Germany) was used to track the position of the head as well as the position of the hands of participants, in order to update the 3D visual scene in response to the head changes and enable action execution and task responses of the participants by using their hands.

4.3.3. Procedure

Pratice Trials: At the beginning of all experiments, participants put on hand-tracker and motion-tracked shutter glasses that were synchronized to the refresh rate of the projector. Then they were shown how to answer which actions they perceived in the experiment by moving their tracked hands and touching one of the two virtual 3D-buttons appearing mid-air labelled with the respective names of the actions ("Giving", "Throwing", "Taking", "Catching"). Participants learned to categorize ambiguous actions as either "Giving" vs. "Throwing" or "Taking" vs. "Catching" depending on the morphs of ambiguous actions ("Giving–Throwing" or "Catching–Taking" action morphs). They were able to practice this repeatedly while different morph weights between the actions were presented in ascending and descending manners in order to determine the point of overall ambiguous perception (PSE) for each participant. All morph levels were presented twice.

Baseline Condition: After the morph weight was determined in the practice trials, participants were presented three repetitions of each test morph stimuli in the absence of adaptor stimuli (baseline). The participants who showed inconsistent responses – e.g. having constantly varying decision criteria – in these three iterations of the same action morphs were considered as ineligible for the experiment and excluded. We determined the baseline perception for each action, and for each participant. Once determined, the morph weights in the test stimuli were kept identical for each participant across all experimental blocks for the rest of the whole experiment. The total number of trials in the baseline condition resulted of 42 trials (2 action morphs × 7 morph levels × 3 repetitions) for each participant.

Main Adaptation Experiment: The main adaptation experiment consisted of eight experimental blocks, a fully crossed design with the factors adaptor stimuli ("Giving", "Throwing", "Taking", and "Catching") and test morphs ("Giving-Throwing" or "Catching-Taking" action morphs). The order of experimental blocks was completely balanced across all participants. Each adaptor stimuli was presented in a separate experimental block. The order of test stimuli presentation within each experimental block was completely randomized. Each experimental block of trials consisted of an initial adaptation phase where the same adaptor stimulus was repeatedly presented 30 times with an inter-stimulus interval (ISI) of 250 ms. Then the main action categorization phase followed directly with a repeatedly presented adaptor stimulus (4 repetitions, ISI of 250 ms) each trial. Each trial ended with a 2-Alternatives-Forced-Choice (2AFC) task where participants had to judge which action they perceived from the presented test stimuli. The ISI between the adaptor stimuli and test stimuli were 400 ms. The next trial started as soon as the participants gave their answer by touching the virtual button by moving their hands. The total number of trials for the main adaptation experiment was 168 trials (8 experimental blocks × 7 morph levels × 3 repetitions of test stimuli) for each participant. Participants took about 75 minutes to finish the whole experiment, taking approximately 5 minutes per experimental block. At the end, every participant filled out a feedback questionnaire with general questions about the experiment (e.g. “Did you use a specific strategy to answer the questions? If yes, please write down your strategy here.”).

4.4. Results

We compared adaptation aftereffects for “Normal-Adaption” and “Cross-Adaption” conditions. “Normal-Adaptation” conditions described the trials measuring direct adaptation aftereffects for each action; i.e. when participants were repeatedly exposed to the same action they had to judge in the trials, such as repeatedly seeing “Giving” in a block of trials then answering whether they recognized “Giving” or “Throwing” from the ambiguous test morph stimuli. “Cross-Adaptation” conditions described the trials measuring the adaptation aftereffects for complementary actions; i.e. when participants were repeatedly exposed to one action from an interaction, but had to judge from morphs of complementary actions, such as repeatedly seeing “Giving” in a block of trials then answering whether they recognized “Taking” or “Catching” from the ambiguous test morph stimuli.

4.4.1. “Normal-Adaption” condition

We found individual adaptation aftereffects for all four actions in “Normal-Adaptation” conditions (Figure 2A). We measured action adaptation aftereffects for each action by subtracting the proportion of responses given to an action in each adaptor condition from the proportion of the responses given to the same action in the baseline condition. In the Normal-Adaptation condition, the adaptation aftereffects for the actions “Giving” and “Throwing” were measured on the “Giving-Throwing” action morph (Figure 1C), therefore calculated as the proportion of “Giving” responses increased after adaptation. The adaptation aftereffects for the actions “Taking” and “Catching” were measured on the “Taking-Catching” action morph (Figure 1C), therefore calculated as the proportion of “Taking” responses increased after adaptation. The direction of the adaptation aftereffect for each action (+ or -) was therefore always indicative of the interaction from which the actions were originally recorded. Perception was consistently shifted in an antagonistic way so that adaptation to an action from Interaction 1 always resulted in more responses towards an action from Interaction 2, and vice versa. Planned one-Sample t-tests confirmed highly significant adaptation aftereffects for all actions in all "Normal-Adaptation" conditions: "Giving" ($t(24) = -4.73$, $p < 0.001$), "Throwing" ($t(24) = 7.9$, $p < 0.001$), "Taking" ($t(24) = -4.65$, $p < 0.001$), "Catching" ($t(24) = 6.72$, $p < 0.001$).

4.4.2. "Cross-Adaption" condition

We found individual adaptation aftereffects for two out of the four actions in "Cross-Adaptation" conditions (Figure 2B). We measured action adaptation aftereffects for each action by subtracting the proportion of responses given to an action in each adaptor condition from the proportion of the responses given to the same action in the baseline condition. In the Cross-Adaptation condition, the adaptation aftereffects for the actions "Giving" and "Throwing" were measured on the "Taking-Catching" action morphs (Figure 1C), therefore calculated as the proportion of "Taking" responses increased after adaptation. The adaptation aftereffects for the actions "Taking" and "Catching" were measured on the "Giving-Throwing" action morphs (Figure 1C), therefore calculated as the proportion of "Givng" responses increased after adaptation. The direction of the adaptation aftereffect for each action (+ or -) was still indicative of the interaction from which the actions were originally recorded (Figure 2B). Perception was consistently shifted in an antagonistic way so that adaptation to an action from Interaction 1 always resulted in more responses towards an action from Interaction 2, and vice versa. Planned one-Sample t-tests confirmed significant adaptation aftereffects for the actions "Giving" ($t(24) = -2.62$, $p = 0.015$) and "Catching" ($t(24) = 3.38$, $p= 0.002$), but not for the actions "Throwing" ($t(24) = 1.21$, $p = 0.24$) and "Taking" ($t(24) = -0.70$, $p= 0.492$).

4.4.3. “Normal-Adaption” vs. “Cross-Adaptation” conditions

We found significant overall adaptation aftereffects for both “Normal-Adaptation” and “Cross-Adaptation” conditions, regardless of which action morphs were used as test stimuli (Figure 3). We measured the overall adaptation aftereffects by subtracting the proportion of responses when the adaptor action was an action from Interaction 1 (e.g. “Giving) from the proportion of responses when the adaptor action was an action from Interaction 2 (e.g. “Throwing”) for each set of morphed actions used as test stimuli. Both the “Normal-Adaptation” condition (“Giving-Throwing” action morphs: t(24) = 10.25, $p < 0.001$, “Taking-Catching” action morphs: t(24) = 11.66, $p < 0.001$) and “Cross-Adaptation” condition (“Giving-Throwing” action morphs: t(24) = 5.63, $p < 0.001$, “Taking-Catching” action morphs: t(24) = 3.9, $p < 0.001$) were significantly different compared to the baseline condition. A two-way repeated measure analysis of variance (ANOVA) on the adaptation aftereffects yielded a significant main effect of adaptation condition (F(1,24) = 56.32, $p < 0.001$), with no significant effect for the morphed actions, and no interaction, Fs < 1. Post hoc comparisons with paired samples t-tests also showed no significant differences between “Giving-Throwing” and “Catching-Taking” action morphs (“Normal-Adaptation”: t(44) = 1.13, p = 0.27, “Cross-Adaptation”: t(42) = -0.04, p = 0.97).

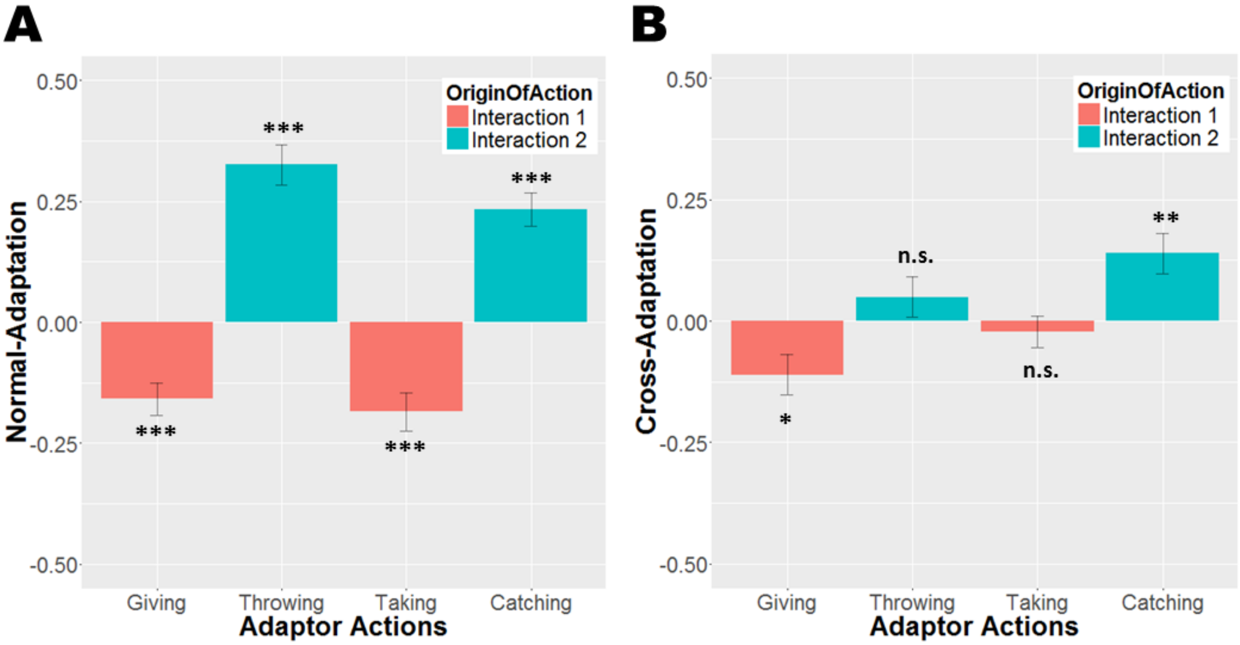

Figure 4-2. Individual adaptation aftereffects for each action. A. "Normal-Adaptation" All actions used as adaptor stimuli showed significant adaptation aftereffects. **B. "Cross-Adaptation"** Only half of the actions used as adaptor stimuli showed significant aftereffects. The y-axis indicates the shift of perception compared to baseline and baseline is defined as zero.

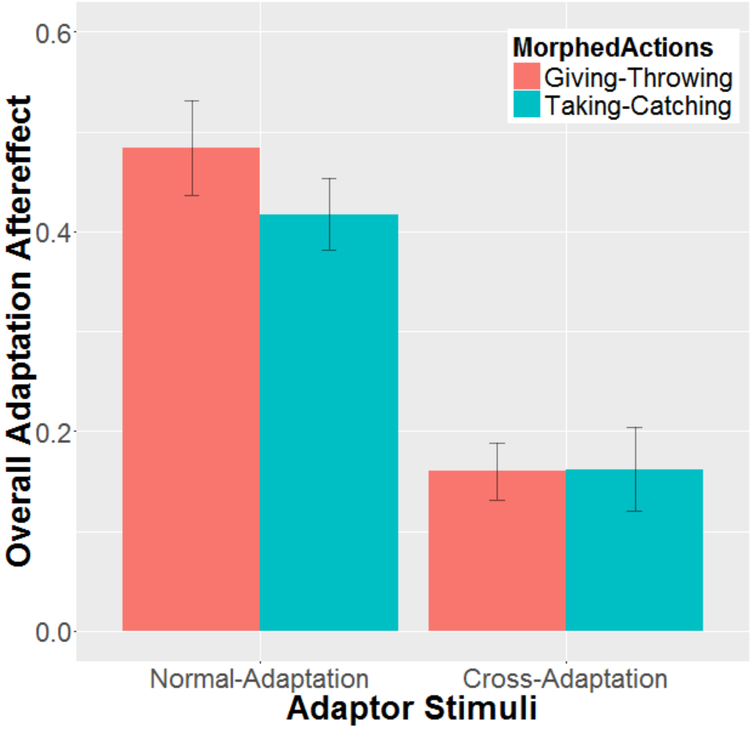

Figure 4-3. Overall adaptation aftereffects in "Normal-Adaptation" vs. "Cross-Adaptation" conditions. The overall adaptation aftereffects were significant across all adaptor conditions, even when the adaptor and test stimuli were not directly overlapping and only complementary actions were used as adaptor stimuli. The y-axis indicates the shift of perception compared to baseline and baseline is defined as zero.

4.5. Discussion

In the present study, we wanted to investigate whether the representation of one action is coupled to the representation of another action performed by an interaction partner in the context of dyadic social interactions. We presented two pairs of complementary actions – four different actions – recorded from two real life dyadic social interactions to participants. Using a visual adaptation paradigm, we compared adaptation aftereffects of an action – "Normal-Adaptation" – to adaptation aftereffects of complementary actions – "Cross-Adaptation" – and found that visual adaptation to one action in a dyadic interaction induces a comparable adaptation aftereffect for a complementary action within the same interaction. These findings suggest that representations of complementary actions are shared in the context of dyadic social interactions.

Our results are one of the first to show the underlying mechanisms behind social action recognition, and contribute new knowledge about how seeing only a part of an interaction could already lead to the knowledge of the whole interaction. We show how the recognition of actions is facilitated in the context of social interactions, and can explain our initial example of why actions affording a social interaction would almost automatically trigger complementary actions: because similar underlying processes are involved for the representation of those actions. However, it is obvious that not all processes are shared, since the magnitude of the overall action adaptation aftereffects are smaller in the "Cross-Adaptation" condition, compared to the "Normal-Adaptation" condition, and also some of the individual actions measured in the "Cross-Adaptation" condition did not show significant aftereffects (Figure 4-2B). An interesting observation is also that we found no significant differences between the adaptation aftereffects of "initiating" actions ("Giving" or "Throwing") and "responding" actions

(“Taking” or “Catching”), regardless of whether “initiating” or “responding” actions were presented as test stimuli (Figure 4-3). These results imply that people are able to recognize an interaction only by seeing a latter part of an interaction (e.g. seeing “Catching” is sufficient to figure out an unseen “Throwing” action). This means that the information retrieved from seeing one person performing an action is already sufficient to predict the complementary action performed by another interaction partner, regardless of whether a complementary action was performed in the past or will be performed in the future. The fact that we do not need to fully know what action the other interaction partner has performed gives us more flexibility in the choice of our own actions, which in turn makes us better in predicting the next actions of others. These findings would complement previous findings on “interpersonal predictive coding” by extending them more broadly to situations of social interactions where both “initiating” and “responding” actions can be predicted from each other by visual information retrieval, and furthermore suggest a underlying mechanism that can overcome mere mirroring or simulation of actions to complementary actions (Manera et al., 2013; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Sartori et al., 2013; Sartori & Betti, 2015).

4.5.1. Shared representations for the alignment between interacting individuals

Why do we need shared representations in the context of dyadic social interactions? When two individuals interact with each other, alignments between the individuals are required both at the behavioral and neural level for the dyadic social interaction to be successful (Hari, Himberg, Nummenmaa, Hämäläinen, & Parkkonen, 2013; Hasson, Frith, & Frith, 2016). Behavioral alignment encompasses all processes involved in the dynamic coordination of actions between the interaction partners, including complementary or mirrored movements, mutual adjustments of motion trajectories, or taking the roles of leader or follower depending on the context (Becchio, Sartori, &

Castiello, 2010; Castiello et al., 2010; Galantucci & Sebanz, 2009; Marsh, Richardson, & Schmidt, 2009; Sartori & Betti, 2015; Sebanz, Bekkering, & Knoblich, 2006). Neural alignment comprises of all shared neural processes concurrently activated in the brains of interacting partners, including a number of different brain networks processing attention, emotions, decision-making, or even higher-level aspects such as reading the goals and intentions of other people’s actions (Hari & Kujala, 2009; Iacoboni et al., 2005; Kokal et al., 2009; Oberwelland et al., 2016; Rizzolatti & Craighero, 2004; Schilbach et al., 2006). In both cases of behavioral and neural alignment, responses across two individuals can only be similar and aligned when the meaning of actions are shared across brains in a specific way (Hasson et al., 2016). In other words, shared representations of the underlying cognitive and neural processes might be indispensable to generate a common ground in social interactions and to make both individuals understand each other (Becchio & Bertone, 2004; Decety & Sommerville, 2003; Gallese, 2003; Gallotti & Frith, 2013a; Hasson et al., 2016; Sebanz et al., 2005; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Tuomela, 2000).

4.5.2. Theoretical implications of shared action representations in social interactions

Are shared representations of actions in dyadic social interactions absolutely necessary? Currently, two different theories of social cognition would take different point of views. According to the interaction-based approaches and second-person views to social cognition, social interaction as a sum encompasses more than the parts of an interaction (De Jaegher, Di Paolo, & Gallagher, 2010; Hari, Henriksson, Malinen, & Parkkonen, 2015; Michael, 2011; Schilbach et al., 2013). From this point of view, it makes more sense that representations in an interaction are encoded for a whole “interaction”, not only for single actions of each actor. In other words, shared representations could count as the default mode for encoding interactions. Real life examples from dancing would support this claim. For example, in Lindy Hop, a partner dance originating from the 1930s, there is a basic move called “swing-out” which can only be danced together by two dance partners – a leader and a follower. Interestingly, this move can never be properly learned or practiced alone, because the physics underlying this move requires that both dance partners perform their parts of the move. Even when each partner performs parts of the steps and turns, just adding the moves of each partner together would not make a real “swing out”, because the real move can only be danced together when both dancers are connected with each other. How would our brains encode a representation for such a particular dance move? This example illustrates that it would make more sense for the brain to encode a representation for the whole dance including the movements of both dance partners rather than only encoding single action sequences for each dancer.

More classical and individual-centered views on social cognition would object the idea that shared representations are by default necessary for encoding interactions (Frith & Frith, 2006a, 2006b, 2007; Gallotti & Frith, 2013b). They would argue that each brain encodes its environment with the primary goal to make sense about the physical world we live in, and social interaction is just part of this bigger environment we have adapted to. More importantly, they point out that shared representations of actions can exist with only potential, or even without interactions, and therefore these representations of actions are not fundamentally different in interactions. From this point of view, shared representations of actions are formed by repeated observation and associative learning. For example, the actions of “Throwing” and “Catching”, or “Giving” and “Taking” have a high chance of co-occurring in most observed cases of everyday life. Thus, shared representations of these complementary actions would be explained by repetitively learned stimulus-response mappings and joint stimulus-response contingencies which every individual has learned through previous experience (Cook et al., 2014; Cooper, Cook, Dickinson, & Heyes, 2013b; Frith & Frith, 2006a, 2006b; Gallotti & Frith, 2013b; Pfister, Dolk, Prinz, & Kunde, 2013; Press, Heyes,

& Kilner, 2011; Sebanz et al., 2005). This interpretation would be also consistent with previous evidence indicating that humans encode their actions in terms of their effects and consequences, also dependent on the learned context (de la Rosa & Bülthoff, 2014; de la Rosa, Streuber, et al., 2014; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Hommel, 1993; Kiernan, Ray, & Welsh, 2012; Kunde, 2001; Pfister, Dolk, et al., 2013).

4.5.3. Generalizability Question and Future Studies

The results of the present study raise several new questions which are worth to discuss and relevant to consider for future investigations. First of all, an important open question is how specific the representation of actions would be in general. If actions in social interactions share underlying representations, how about other actions which also occur in close spatiotemporal proximity? Is it possible that the brain employs these shared representations as a general efficient mechanism to categorically encode similar, contingent actions? In order to construct an "action map" in the future to more broadly investigate how different actions are represented in the brain, answering this question would be one of the most important future tasks. Second, another question would be whether our findings might extend to different and more complex actions. Previous studies have shown that adaptation paradigms offer a useful tool to investigate action representations with more naturalistic social actions (de la Rosa et al., 2014, 2016). However, the adaptation paradigm we applied in our present study was mainly visual, and we did not directly examine motor representations. In order to extend our findings to more complex actions, further assessing both visual and motor representations would be necessary since the interaction between both visual and motor domains for action representations is a hotly debated topic and it is still unclear whether co-representation of actions involve both visual and/or motor representations in interactions (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Giese & Rizzolatti, 2015). Moreover, it would be necessary to further examine dyadic interactions within different social contexts – e.g. competitive vs. cooperative – since it has been previously shown that representations of actions are strongly modulated by social contexts (de la Rosa, Streuber, et al., 2014; Streuber, Sebanz, Knoblich, Bülthoff, & de la Rosa, 2011). It would be also interesting to investigate actions which are not only more complex but also strictly choreographed – e.g. professional partner dance moves such as in Salsa, Tango or Swing Dance – in order to compare representations of these actions in expert dancers and naïve participants. One could predict that shared representations of actions in interactions also depend on learning and expertise, so that naïve participants show less or almost no co-representation of those actions requiring extensive learning.

What other factors could potentially influence the shared representation of actions? Every interaction is dependent on specific contexts which cannot be generalized, meaning that the nature of the interaction could only be determined by many other factors such as the participating interaction partners, familiarity and sympathy between interaction partners, and the exact interaction task, e.g. whether a ball, or a book, or a Frisbee is thrown. The different ways how the stimuli are presented could also play a critical role, such as the spatial distance between the actors while recording the interaction, different viewpoints of the presented actions, and temporal distances between the presented actions (inter-stimulus-intervals) and other factors affecting the perceived contingencies between the actions. Based on the experimental paradigm tested in our present study, future studies should aim to further investigate these factors.

4.6. Conclusion

We found that observation of an action activates concurrent processes during the observation of complementary actions specific to action pairs within an interaction. These findings demonstrate that representation of actions are shared in the context of dyadic social interactions and allow new insights about how humans can so successfully coordinate their actions together. Shared representations of actions may provide an effective anticipatory mechanism for humans to understand others' actions and to engage in more complex social interactions. Future studies should further elucidate how shared representations can contribute to theories of social cognition and how we understand each other in interactions.

4.7. Acknowledgments

We thank Ylva Ferstl for the recording and processing of the motion-captured action stimuli, Monika Marsching and Anne Thaler for their consideration and support while using the augmented reality setup in the backpro lab. We especially thank members of the Social & Spatial Cognition Group – Tobias Meilinger, Laura Fademrecht, Aurelie Saulton, Thomas Hinterecker, Marianne Strickrodt – and Christian Wallraven, Stephan Streuber, Alejandra Quiros for their helpful discussions and support.

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5 The Perception of Cooperativeness Without Any Visual or Auditory Communication

This chapter has been reproduced from an article published in the journal *i-Perception*: Chang, D-S., Burger, F., Bülthoff, H.H. & de la Rosa, S. (2015). The Perception of Cooperativeness Without Any Visual or Auditory Communication. *i-Perception*, doi:10.1177/2041669515613671.

5.1. Abstract

Perceiving social information such as the cooperativeness of another person is an important part of human interaction. But can people perceive the cooperativeness of others even without any visual or auditory information? In a novel experimental setup, we connected two people with a rope and made them accomplish a point-collecting task together while they could not see or hear each other. We observed a consistently emerging turn-taking behaviour in the interactions and installed a confederate in a subsequent experiment who either minimized or maximized this behaviour. Participants experienced this only through the haptic force-feedback of the rope and made evaluations about the confederate after each interaction. We found that perception of cooperativeness was significantly affected only by the manipulation of this turn-taking behaviour. Gender- and size-related judgments also significantly differed. Our results suggest that people can perceive social information such as the cooperativeness of other people even in situations where possibilities for communication are minimal.

5.2. Introduction & Results and Discussion

Perceiving social information of an interaction partner is crucial for human interaction (C. D. Frith & Frith, 2007; Leonhard Schilbach et al., 2013). Especially, being able to perceive whether another interaction partner is cooperative or competitive seems to be important for effective real-time coordination with interaction partners (Pfeiffer et al., 2011; Streuber et al., 2011). Previous studies have also shown how non-verbal forms of communication such as eye gaze, gestures or kinematics play an important role for successful interactions (Kuhlen, Galati, & Brennan, 2012; Pezzulo, Donnarumma, & Dindo, 2013; Pfeiffer et al., 2011). However, studies investigating real-time interaction without the exchange of social information conveyed by visual or auditory channels have been rare, and we wanted to test this in a situation where possibilities for communication were minimalistic.

How do people perceive the cooperativeness of others if possibilities to exchange visual or auditory information are limited during real-time interactions? Theories of human cooperation would predict that humans have clear beliefs and expectations about the behavior of others, so that individuals complying with these expectations would be seen as more cooperative (Fehr & Fischbacher, 2004; Tomasello et al., 2005b). Humans also seem to have a default expectation of reciprocity and judge the cooperativeness of others based on this presumed disposition of interaction partners (Pfeiffer et al., 2011). The same theories would also predict that humans make person-related inferences about interaction partners even when not much information is present, since inferring the intentions of a partner is natural to almost any human interaction.

In the present study, we connected two participants with a rope and they had to accomplish a joint task together. The task consisted of collecting points on a laptop computer which was located on each side and could only be reached if both interaction partners coordinated their movements (Fig 5-1). Importantly, participants were separated by a visual barrier and used a noise-cancelling headphone so they could not see or hear each other in order to make direct communication impossible. The only source of information about the other partner was the haptic force-feedback conveyed through the rope during the simultaneous joint coordination. During the first pilot trials (4 dyads, n=8), we observed a consistently emerging reciprocal "turn-taking behaviour". Although multiple coordination patterns were possible, it seemed as participants were automatically expecting their partners to collect their points alternately and take turns. We wanted to test whether this "turn-taking behaviour" was associated with perception of cooperativeness and installed a confederate who either maximized or minimized this behaviour. Furthermore, do participants make person-related inferences about their interaction partner even when possibilities for communication are minimalistic?

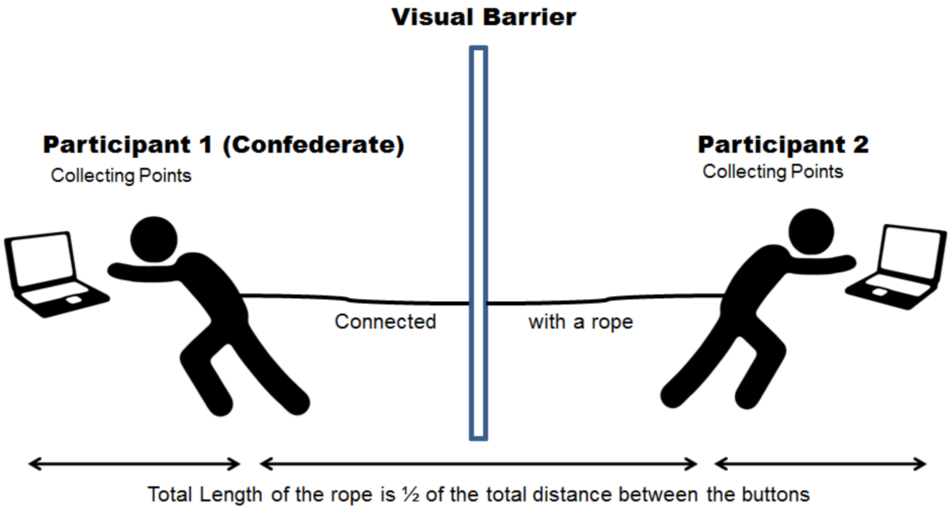

Figure 5-1. Joint Task A dyadic pair had to collect points together by pressing eight buttons (A-H) in the right order on a laptop located on each side. All participants were separated by a visual barrier. Points were paid out as money proportional to the collected number of points, but only if both participants successfully finished collecting the specified number of points.

We tested 24 participants (f=12, m=12) who interacted with the same confederate in two sessions while they believed that they interacted with different partners in the two sessions. The confederate maximized "turn-taking" (being fast and predictive with alternating the collection of points) in one, and minimized "turn-taking" (being slow and reluctant to alternating the collection of points) in the other session. The order of the sessions was balanced. After each session, participants rated the cooperativeness of the interaction partner on a Likert scale (1-7), and gave estimates about person-related attributes such as the gender and size of their interaction partners.

The results showed that perceived cooperativeness of the interaction partner significantly differed (t(23)=-7.11, p<0.001) depending on whether the interaction partner was engaging in "turn-taking behavior" (M=6.38, SD=1.28) or not (M=3.63, SD=1.47) (Fig 5-2).

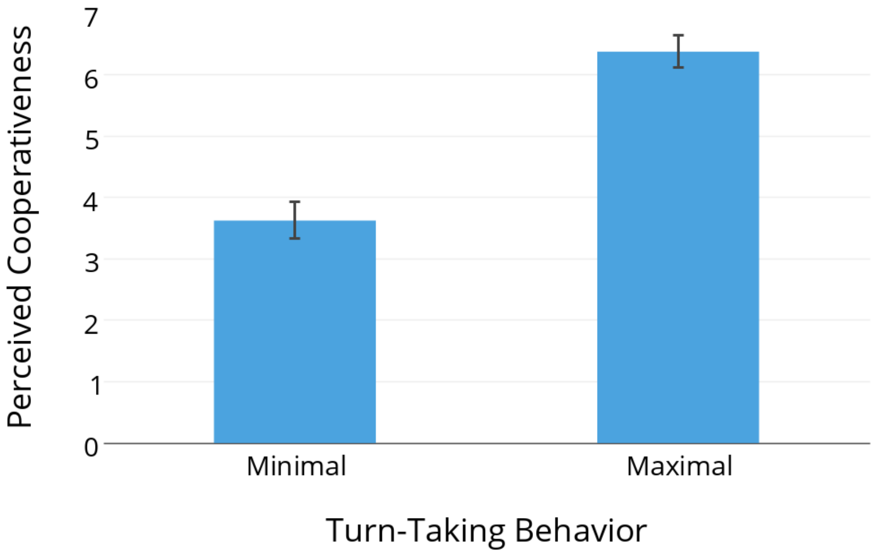

Figure 5-2. Perceived Cooperativeness We compared minimizing or maximizing the "turn-taking behaviour" of the interaction partner. Error bars are depicted as standard error of the mean.

Moreover, participants made different person-related inferences about the gender and size of the confederate (Fig 5-3). Cooperative partners were more often perceived as female, whereas less cooperative partners were more often perceived as male (t(41)=-3.53, p<0.01). The perceived body size of interaction partners was also significantly different dependent on the partner's behavior. (t(24)=1.29, p <0.001).

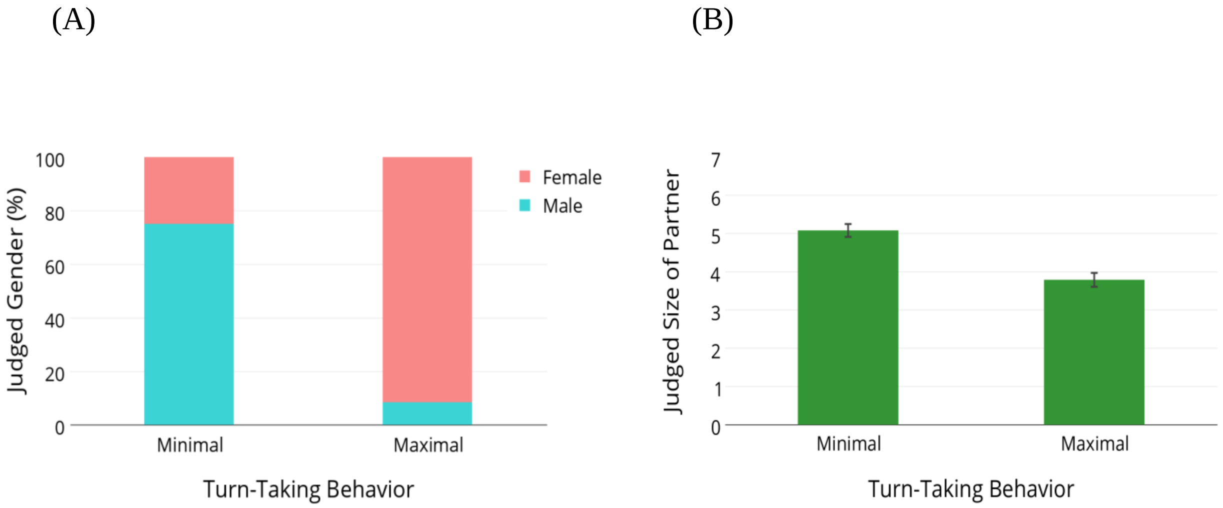

Figure 5-3. Person-related Inferences (A) Judged gender of the interaction partner. (B) Judged size of the interaction partner. Error bars are depicted as standard error of the mean.

In summary, our results suggest that people collect social information and make inferences about their interaction partner even when possibilities for communication are minimalistic. It is noteworthy that a reciprocal "turn-taking behavior" automatically emerged in the interactions, and manipulating this behavior influenced the perception of cooperativeness as well as person-related inferences of the partner. Furthermore, our experimental paradigm of directly connecting two individuals and only allowing haptic force-feedback could serve as a useful method to further study how joint motor coordination is coupled to the perception of social information.

5.3. Acknowledgements

We would like to thank Stephan Streuber, Aurelie Saulton, Laura Fademrecht and Martin Breidt for the useful discussions on the design of the experiment and tips for the preparation of the manuscript. This research was supported by the Max Planck Society and part of the research was supported by the Brain Korea 21 PLUS Program through the National Research Foundation of Korea funded by the Ministry of Education.

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